

# Winter severity influences spotted seatrout mortality in a southeast US estuarine system

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**ABSTRACT:** Winterkill in spotted seatrout *Cynoscion nebulosus* is associated with extreme cold conditions throughout much of the species' geographic range. However, rigorous study is needed to confirm longstanding but largely untested assumptions that acute cold stress drives overwinter loss. We provide the first direct field-based estimates of spotted seatrout survival relative to the severity of cold temperatures. Spotted seatrout overwintering in North Carolina, USA, estuaries were tagged with ultrasonic transmitters and monitored during 3 consecutive and variable winters from 2009 to 2012. Fates of telemetered fish were inferred from daily movements and used in a multistate capture-recapture model to estimate instantaneous rates of natural mortality ( $M$ ), fishing mortality, and emigration. Natural death was inferred for 7 fish in 2009/2010 ( $n = 34$  telemetered spotted seatrout at risk), 6 fish in 2010/2011 ( $n = 9$  fish at risk), and 1 fish in 2011/2012 ( $n = 65$  fish at risk), and when estimable, weekly  $M$  ranged from 0.001 to 0.187. Daily estimates of natural mortality increased quickly with declining water temperatures ( $T$ ),  $M = 1/[1 + e^{-(0.714 - 0.756T)}]$ , and indicated that cold-stun deaths occurred when water temperatures were below  $\sim 7^\circ\text{C}$ . Our results provide direct evidence that winterkill in spotted seatrout at its northern limits of distribution is related to the severity of low water temperatures and demonstrate that the simultaneous monitoring of telemetry-tagged animals and abiotic conditions is an effective approach to determine lethal environmental limits.

**KEY WORDS:** *Cynoscion nebulosus* · Telemetry · Multistate · Capture-recapture · Survival · Winterkill · Cold tolerance · Temperature-dependent mortality · Mortality rate

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## INTRODUCTION

There has been much ecological research focused on overwinter mortality in juvenile fishes (reviewed by Hurst 2007). However, quantitative examination of overwinter mortality in adult fishes has received much less attention despite a long history of anecdotal reports of mass mortality events in temperate estuaries during harsh winter conditions (e.g. Wilcox 1886, Dahlberg & Smith 1970, McEachron et al. 1994); hereafter, we refer to these events as winterkill. The emphasis on juveniles is understandable given the importance of this stage in setting year-

class strength in fishes, but determining the sources and magnitude of mortality in adult fishes can also be critical to understanding fluctuations in population size. *In situ* studies of fish cold tolerance present numerous challenges, most notable of which are the ability to link a history of the thermal dynamics experienced by individuals to some stressful endpoint (e.g. death) and timing of such field research with extreme variability in winter temperatures. This is likely why there are few field-based studies that have directly estimated the impact of winterkill in adult temperate fishes (e.g. Adams et al. 2012). Detailed and continuous monitoring of the fates of

fish and the thermal conditions they experience is essential given the episodic and acute nature of winterkills.

Additionally, an improved understanding of natural mortality during winter is important to successful management of many exploited fish populations. Population models used in fisheries science rely on accurate information regarding the sources and levels of mortality affecting abundance. Traditional age-structured stock assessment techniques are generally sufficient for estimating the total instantaneous mortality rate ( $Z$ ) but often lack sufficient data to accurately partition  $Z$  into its fishing ( $F$ ) and natural ( $M$ ) components (Quinn & Deriso 1999). Natural deaths are seldom observed, and our knowledge of  $M$  is often limited to proxy estimation from life-history correlates (e.g. Hoenig 1983, Lorenzen 1996, Then et al. 2015), or more preferably, indirect estimation through tag-return methods that require reliably estimated auxiliary tagging parameters (i.e. tag-reporting rate, tag retention, tagging-induced mortality) in order to precisely determine  $F$  and  $M$  (Hoenig et al. 1998, Pollock et al. 2001). However, it is usually not possible to link the specific timing and sources of disturbance (e.g. unusually low winter temperatures) to tag-return estimates of  $M$ .

Acoustic telemetry data are increasingly being used to estimate fish mortality rates (Hightower et al. 2001, Heupel & Simpfendorfer 2002, Bacheler et al. 2009, Topping & Szedlmayer 2013). The general approach involves relocating telemetered individuals in a defined study area through active (i.e. manual searches) and passive (i.e. stationary receiver arrays) tracking until 1 of 4 possible final fates is determined: natural mortality; harvest; emigration; or transmitter failure (e.g. expired battery) (Hightower et al. 2001). Important advantages of telemetry over tag-return methods are (among others) (1) relocation probabilities of telemetered fish that greatly exceed typical recapture probabilities of fish with conventional tags and (2) auxiliary information on tag-reporting rate is not required to estimate  $F$  and  $M$  (Pine et al. 2012). Furthermore, the direct estimates of  $M$  provided by telemetry at fine spatial and temporal scales can be related to likely sources of natural mortality such as suboptimal abiotic conditions.

Winterkill in spotted seatrout *Cynoscion nebulosus*, an estuarine-dependent and economically important sportfish in the US South Atlantic and Gulf of Mexico, has been well documented across much of the species' range (Storey & Gudger 1936, Gunter & Hildebrand 1951, Moore 1976, McEachron et al. 1994, NCDMF 2012), beginning as early as 3 cen-

turies ago (Lawson 1709). However, loss of spotted seatrout due to winterkill has only recently been estimated. The mortality rates of spotted seatrout have been shown through tag-return data to vary seasonally at the northern extent of the species' geographic range (North Carolina and Virginia, USA), with  $M$  generally higher during winter (Ellis 2014). At this northern distribution, many spotted seatrout overwinter in relatively shallow habitats of the upper estuary where encroaching arctic air masses periodically expose fish to rapid declines in water temperature. Direct study of winter  $M$  for spotted seatrout, including environmental monitoring at a fine temporal scale, is needed to confirm longstanding but largely untested assumptions that acute cold stress drives overwinter loss.

The purpose of this study was to examine the survival of spotted seatrout during winter in a southeast US estuarine system through *in situ* monitoring of localized abiotic conditions and telemetered fish movements. Our objectives were to (1) estimate fishing mortality, natural mortality, and emigration rates for spotted seatrout during winter in these habitats using telemetry; (2) determine the importance of acute cold stress relative to other potential sources of natural mortality on overwinter loss of spotted seatrout at its northern limit of distribution; and (3) develop a relationship between winter temperature and the natural mortality of spotted seatrout. In addition to the findings for spotted seatrout, our study demonstrates the utility of combining telemetry and environmental monitoring to better understand the survival response to abiotic conditions.

## MATERIALS AND METHODS

### Telemetry study sites

Telemetry of spotted seatrout occurred throughout 3 winters from 2009 to 2012 within overwintering habitats of the Pungo and Neuse Rivers, both major tributaries of Pamlico Sound, North Carolina. Study sites were Pantego Creek, Pungo Creek, Slocum Creek, and Hancock Creek (Fig. 1). These study sites are relatively shallow with uniform depths averaging 1–3 m with some areas of deeper water (e.g. 3–6 m). Due to their distance from ocean access, lunar tides are negligible in these tributaries, and wind mixing and precipitation regulate salinities between oligohaline and mesohaline conditions (Giese et al. 1979). A large section of Pungo Creek is open to commercial fishing, but harvest of spotted seatrout is limited to

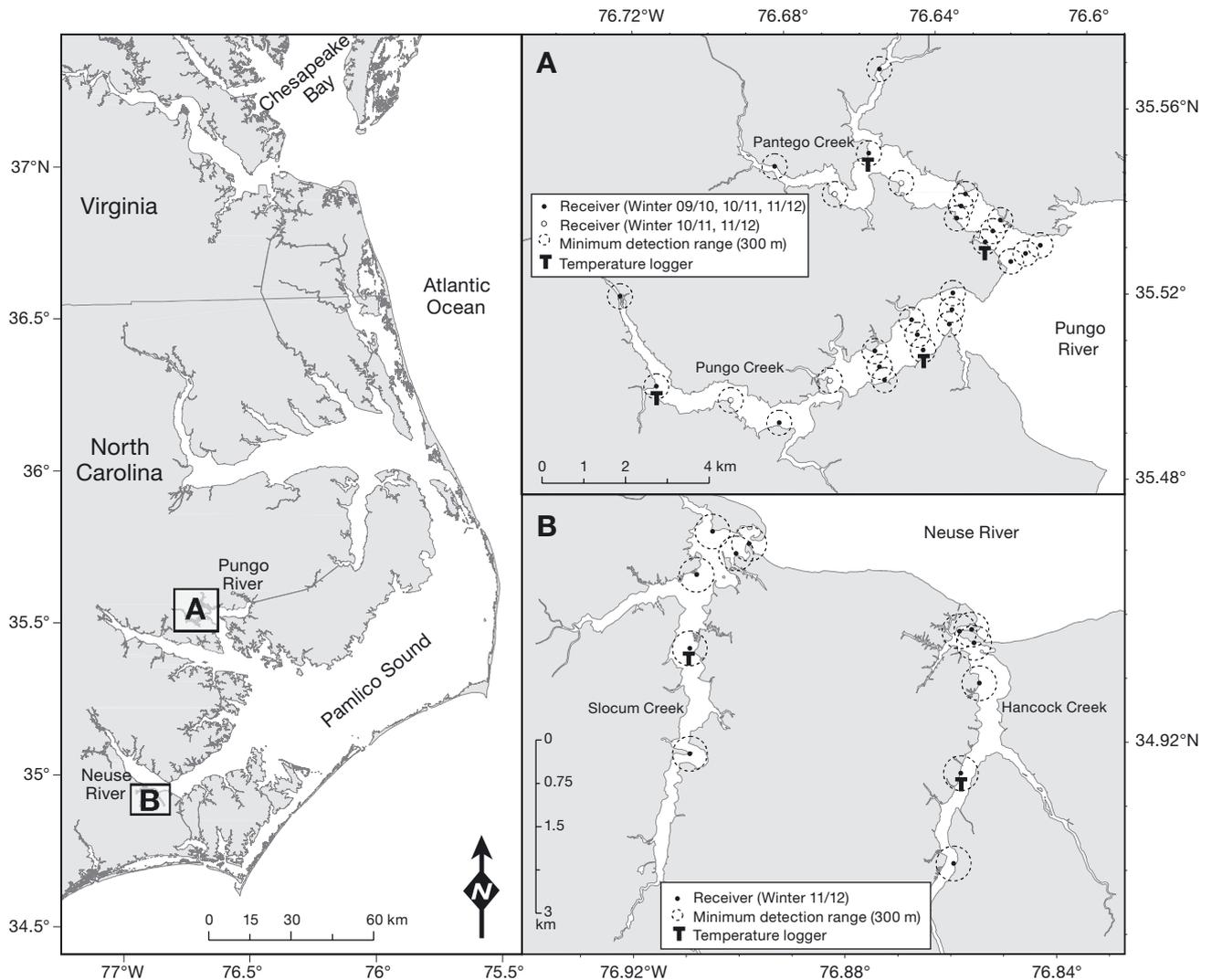


Fig. 1. Study sites in North Carolina, USA (A: Pungo River tributaries; B: Neuse River tributaries), where spotted seatrout were monitored with acoustic telemetry across 3 separate winters: 2009/2010, 2010/2011, and 2011/2012

the recreational fishing sector in the other 3 study sites. Hydrographical features of these areas, including their shape and size, permit the frequent tracking of telemetered fish by active and passive techniques on manageable temporal and spatial scales (see 'Telemetry relocations' below). Additionally, spotted seatrout have historically been abundant in these tributaries during winter, which are periodically prone to extreme low temperatures.

### Transmitter implantation

In November–February 2009–2010, 2010–2011, and 2011–2012, spotted seatrout were captured primarily using hook-and-line. In the Neuse River study sites, some fish were obtained by electrofishing.

Healthy individuals (i.e. no physical signs of stress from capture techniques) that met a pre-determined minimum total length (TL) requirement of 356 mm were kept as telemetry-tagging candidates. The minimum TL requirement was based on laboratory results (see 'Laboratory estimates of postsurgical survival and transmitter retention' below). All candidate spotted seatrout were immediately placed in onboard holding tanks (at least 100 l in size) containing ambient water. We maintained water quality through frequent water changes, continuous aeration, and supplemental oxygenation as needed. Uniquely coded ultrasonic transmitters (VEMCO; V13-1H, 13 × 36 mm, ~10.5 g in air, 69 kHz frequency, 30 to 90 s random transmission rate, ~196 d battery life) were surgically implanted into telemetry candidates. Some larger candidates (TL > 457 mm) in the Neuse River

study sites received larger transmitters (VEMCO; V16-4H, 16 × 68 mm, ~23.5 g in air, 69 kHz frequency, 60 to 120 s random transmission rate, ~641 d battery life). The surgical procedure employed for implanting fish with transmitters was similar to the guidelines of Wagner et al. (2011) but tailored specifically for spotted seatrout with the assistance of staff from the North Carolina State University (NCSU) College of Veterinary Medicine (CVM) (e.g. Harms & Lewbart 2011). Individual spotted seatrout were anesthetized with 150 mg l<sup>-1</sup> of tricaine methanesulfonate (MS-222), measured (TL; mm) and weighed (wet weight, WW; g), and implanted with a transmitter in the abdominal cavity. The incision was closed with simple interrupted sutures (Ethicon Endo-Surgery, Inc.; PDS II synthetic absorbable suture in 3-0 thread size with FS-1 reverse cutting needle) and the fish was allowed to recover (i.e. reestablish equilibrium and exhibit normal swimming behavior) before release. Total time under sedation ranged from 8 to 12 min, and recovery typically occurred within 10 min of surgery.

### Telemetry relocations

We monitored telemetered spotted seatrout movement within, out of (emigration), and into (immigration) each study site using a stationary array of submersible receivers (VEMCO VR2 and VR2W; hereafter referred to as VR2/W) (Fig. 1). Preliminary range testing was conducted using a fixed-delay V13-1H transmitter and followed the manufacturer's recommended protocol. We determined that these transmitters were fully detected (i.e. 100% of transmissions) at up to 300 m in our study sites. Similar range testing done by Bachelier et al. (2009) in these same habitats determined that V16-4H transmitters were fully detected by VR2/W receivers up to 400 m. Consequently, VR2/W receivers at the mouths of our study sites were conservatively positioned 400 m apart from one another and within 200 m of shore (Fig. 1) in order to observe all emigration and immigration events by telemetered spotted seatrout. Additional VR2/W receivers were systematically stationed in areas upstream of the mouth array to monitor broad daily movement patterns within each study site. Each VR2/W receiver continuously logged the unique transmitter ID code, date, and time of all telemetered spotted seatrout that were within the range of detection for the duration of the study.

Telemetered spotted seatrout were manually relocated within each study site every 7 d during winter months (December to February; more frequently

when water temperatures were ≤7°C) and at least every 14 d during spring months (March to June). Manual tracking in each study site was done using an ultrasonic receiver (VEMCO VR100) equipped with an omnidirectional hydrophone (VEMCO VH165) and involved navigating by research vessel to fixed listening stations (n = 15–30) approximately 100–500 m apart, depending on hydrography. The distance between listening stations was dependent on changes in depth or shoreline orientation, since these can inhibit the detection of a transmitting acoustic signal. Upon general relocation, a unidirectional hydrophone (VEMCO VH110) was regularly used to determine a more precise position of an individual telemetered spotted seatrout. Schooling of spotted seatrout was common, occasionally resulting in overlapping acoustic transmissions by telemetered individuals (which could be heard via the VR100 speaker). Therefore, we listened at each station until the VR100 receiver successfully registered all present unique transmitter identification codes. Time-of-day, latitude, longitude, and depth were recorded at each listening station. If the acoustic signal of any telemetered spotted seatrout was missed during a manual-tracking event, it was considered to be present in the study site at that time if a VR2/W receiver detected it and the fish was determined not to be emigrating (i.e. most recent passive detection was not on outer-most VR2/W array at tributary mouth and occurred prior to manual-tracking event). The tracking of telemetered spotted seatrout each year continued until all fish in a study site died, were harvested, or permanently emigrated (see 'Interpretation and modeling analyses of telemetry data' below for description of telemetered fish fates).

Bottom water temperature was recorded at 15 min intervals using HOBO water temperature Pro v2 data loggers (± 0.2°C accuracy) deployed at 2 (upstream and downstream) VR2/W stations in each of the relatively larger study tributaries of the Pungo River and at 1 (central) VR2/W station in each of the relatively smaller study tributaries of the Neuse River (Fig. 1). All temperature loggers were positioned at a uniform depth of ~1.5 m. We combined temperature and time into a single measure, cumulative degree day (CDD), to characterize minimum thermal tolerance defined by prolonged exposure to some base (e.g. sublethal) low temperature (Wuenschel et al. 2012). We chose a threshold temperature of 7°C based on laboratory results (see Anweiler et al. 2014, Ellis et al. in press). For each telemetry season and study system, the cumulative degree days below 7°C (CDD < 7°C) was calculated as:

$$\text{CDD} < 7^{\circ}\text{C} = \sum_{t=1}^{t=n} (7.0 - \text{Temp}_t) \quad (1)$$

where  $\text{Temp}_t$  is the mean water temperature of day  $t$  for days when  $\text{Temp}_t < 7^{\circ}\text{C}$  and  $n$  is the total number of consecutive days with fish at-risk.

### Laboratory estimates of postsurgical survival and transmitter retention

We undertook a long-term captive study (November 2008 to May 2009) examining tagging mortality and tag retention for spotted seatrout implanted with either an internal anchor tag or an ultrasonic transmitter. Hook-and-line-captured spotted seatrout from polyhaline waters surrounding the NCSU Center for Marine Sciences and Technology in Morehead City, North Carolina (34° 43' N, 76° 45' W) were transported to and randomly distributed among four 1500 l outdoor flow-through holding tanks. Each tank received ~20  $\mu\text{m}$  filtered polyhaline seawater from Bogue Sound at an approximate flow rate of 8 l  $\text{min}^{-1}$  and continuous aeration. Structure in the form of marl blocks was added to the center of each tank, and a half opaque and half light-penetrable plastic screen provided full cover. Fish were fed a combination of locally collected live and freshly dead prey (*Fundulus* spp., penaeid shrimp spp.) 3 times per week. Data loggers (StowAway TidbiT;  $\pm 0.4^{\circ}\text{C}$  accuracy) recorded tank water temperature ( $^{\circ}\text{C}$ ) every 15 min. Additionally, water temperature, salinity, and dissolved oxygen measurements were taken daily for each tank using a temperature-conductivity meter (YSI Model 85). Upon termination of the experiment, all surviving fish were euthanized with a lethal dose (300–400  $\text{mg l}^{-1}$ ) of MS-222, and necropsies were performed under the guidance of onsite NCSU CVM staff to further examine overall health in relation to the presence of an internal anchor tag or ultrasonic transmitter.

A total of 44 spotted seatrout were randomly assigned to 1 of 4 replicate tanks and to 1 of 3 treatments per tank: control ( $n = 16$ , 4  $\text{tank}^{-1}$ ), 1 internal anchor tag ( $n = 16$ , 4  $\text{tank}^{-1}$ ), or 1 transmitter ( $n = 12$ , 3  $\text{tank}^{-1}$ ). The 12 telemetry-tagged spotted seatrout were implanted with dummy transmitters (VEMCO; V13,  $n = 8$ , 2  $\text{tank}^{-1}$ ; V16,  $n = 4$ , 1  $\text{tank}^{-1}$ ) identical in dimensions and weight to those used in the telemetry study and following the surgical procedures described earlier, except that a simple continuous (versus interrupted) suture technique was used to close the incision following transmitter implantation. These fish were added to the experimental tanks 11 d

after the control and conventionally-tagged fish. Therefore, daily observations of tag loss, overall health (e.g. normal swimming and feeding behavior), and mortality were made over periods of 236 d (control and conventional-tag treatments) and 225 d (telemetry-tagged spotted seatrout).

### Interpretation and modeling analyses of telemetry data

Hightower et al. (2001) established conditions for interpreting the fate of a telemetered fish based on its observed movements following release. Possible fates include surgery-related mortality, natural mortality, harvest, emigration, or transmitter failure. Telemetered spotted seatrout were assumed to be alive primarily if their positions varied between manual relocation events. If a telemetered individual was missed during a manual search event, it was assumed to be alive based on movement indicated by detections across multiple stationary receivers or the timing of multiple detections on a single stationary receiver (Harris & Hightower 2011). Alternatively, natural death was assumed for fish whose location remained stationary across multiple searches or whose detection history on a single receiver indicated that the fish was stationary (i.e. not moving in and out of range of the receiver). Data were excluded for a 7 d censorship period following release to ensure that any surgery-related effects on immediate survival and behavior (e.g. higher emigration rates) were not misinterpreted as natural deaths or normal movement patterns. Telemetered spotted seatrout that were detected moving after the censorship period but later not relocated after repeated manual searches of a study area and undetected by the VR2/W receiver array (i.e. did not move within or emigrate from the study area) were assumed to have been harvested (see below for exception when water temperatures were  $\leq 7^{\circ}\text{C}$ ). Swimming speeds of telemetered spotted seatrout (see below) were such that our receiver gates logged multiple detections for individuals leaving our study systems, which allowed for clear assignment of emigration fate.

Avian predation could be misinterpreted as a harvest of a telemetered spotted seatrout from our study sites. Spotted seatrout are a dominant prey species for the osprey *Pandion haliaetus* during its summer breeding season in systems similar to our study sites (Glass & Watts 2009). However, ospreys overwinter in areas south of North Carolina and were uncommon in our study sites over the time periods in which

telemetry took place. Other birds such as gulls (*Larus* spp.) and pelicans (*Pelecanus* spp.), as well as semi-aquatic mammals such as the North American river otter *Lontra canadensis*, may opportunistically feed on lethargic and moribund spotted seatrout suffering from acute cold stress and could remove a telemetered spotted seatrout from the water. Given the inefficiency of traditional fishing gears (e.g. hook and line, gill net) at catching spotted seatrout in low temperatures, the relatively low fishing effort observed in these study sites during cold episodes (other than hand harvesting of moribund fish), and that only immobilized telemetered spotted seatrout provide feeding opportunities for winter avian predators in these study sites, we assumed that the disappearance of a telemetered spotted seatrout during cold conditions (i.e. water temperatures  $\leq 7^\circ\text{C}$ ) resulted from acute cold stress and was therefore interpreted as a natural mortality.

The consumption of a telemetered spotted seatrout by larger predators emigrating from our study sites (i.e. swimming through receiver arrays) could negatively bias estimates of  $M$  and positively bias estimates of emigration if not taken into account (Heupel & Simpfendorfer 2002, Bacheler et al. 2009, Friedl et al. 2013). We assessed the potential for this bias by comparing the swimming speeds of emigrating telemetered spotted seatrout to those reported for bottlenose dolphins (*Tursiops truncatus*; data from Bacheler et al. 2009), known predators of spotted seatrout in North Carolina (Gannon & Waples 2004, Harms & Watts 2010). Emigration swimming speeds for telemetered spotted seatrout were estimated following the approach used by Bacheler et al. (2009) for telemetered subadult red drum *Sciaenops ocellatus* from the same or similar estuarine tributaries.

Telemetry data were analyzed using multistate capture-recapture models (Kéry & Schaub 2012) in which weekly estimates of survival and recapture (detection) probabilities for telemetered spotted seatrout depended upon various possible states ( $s$ ) at sampling time ( $t$ ) and the probability of remaining or transitioning out of a particular state at  $t+1$ . In this study, live fish at week  $t$  could either remain alive ( $s = 1$ ) at week  $t+1$  or transition to either of 3 other possible states: natural death ( $s = 2$ ), emigrated ( $s = 3$ ), or harvested ( $s = 4$ ). Multistate models were fitted in a Bayesian framework using a state-space likelihood that was based on a categorical distribution (Kéry & Schaub 2012). The state-space formulation defined probabilities for both the state-transition and observation matrices (see Supplement 1, [www.int-res.com/articles/suppl/m564p145\\_supp.pdf](http://www.int-res.com/articles/suppl/m564p145_supp.pdf)). Individual tele-

metered spotted seatrout ( $i$ ) were assumed alive ( $s = 1$ ) at the end of the 7 d censorship period, and all subsequently estimated true states,  $z_{i,t}$  were conditional on  $s_{i,t-1}$ . The state-transition probability matrix for the  $i$ th individual was defined as follows:

$$P_{z_{i,t}} = \begin{matrix} & \underline{s_{t+1}=1} & \underline{s_{t+1}=2} & \underline{s_{t+1}=3} & \underline{s_{t+1}=4} & \\ \left\{ \begin{array}{l} \phi_t & M_t(1-\phi_t)/Z_t & E_t(1-\phi_t)/Z_t & F_t(1-\phi_t)/Z_t & \text{when } s_t = 1 \\ 0 & 1 & 0 & 0 & \text{when } s_t = 2 \\ 0 & 0 & 1 & 0 & \text{when } s_t = 3 \\ 0 & 0 & 0 & 1 & \text{when } s_t = 4 \end{array} \right. & & & & \\ \hline & \phi_t = e^{-Z_t} ; Z_t = F_t + M_t + E_t & & & \end{matrix} \quad (2)$$

where  $\phi_t$  was the  $t$ -specific probability of surviving and remaining in the study area and was a function of weekly instantaneous rates of fishing mortality ( $F$ ), natural mortality ( $M$ ), and emigration ( $E$ ). The observed state,  $y_{i,t}$  was conditional on  $z_{i,t}$  and observation types included detected-alive ( $y_{i,t} = 1 \Rightarrow s = 1$ ), detected-natural death ( $y_{i,t} = 2 \Rightarrow s = 2$ ), detected-emigration ( $y_{i,t} = 3 \Rightarrow s = 3$ ), or not detected/unobserved ( $y_{i,t} = 4 \Rightarrow s = 1$  or  $s = 4$ ). The observation probability matrix for the  $i$ th individual was defined as follows:

$$P_{y_{i,t}} = \begin{matrix} & \underline{y_t=1} & \underline{y_t=2} & \underline{y_t=3} & \underline{y_t=4} & \\ \left\{ \begin{array}{l} p_t & 0 & 0 & 1-p_t & \text{when } s_t = 1 \\ 0 & 1 & 0 & 0 & \text{when } s_t = 2 \\ 0 & 0 & 1 & 0 & \text{when } s_t = 3 \\ 0 & 0 & 0 & 1 & \text{when } s_t = 4 \end{array} \right. & & & & \end{matrix} \quad (3)$$

where  $p_t$  was the  $t$ -specific detection probability. The detection information from the combination of passive and active tracking was sufficient for assigning fates for all emigration and natural mortality events, including both stationary transmitters and removals of telemetered fish during cold episodes, and to accurately assign those events to the week in which they occurred. Although the weekly state (i.e. alive or harvested) of any undetected spotted seatrout during non-cold periods was unknown, there was a higher probability of harvest (i.e.  $z_{i,t} = 4$ ) for fish that remained undetected for multiple weekly periods.

Sample size was augmented through a staggered entry design in which both new releases of telemetered fish and immigration back to the study area by fish that previously emigrated contributed to the estimated at-risk population for each week. In addition to the sources of bias affecting the determination of fates for telemetered fish described earlier, several other assumptions apply to our multistate modeling of telemetry data. First, we assumed that movement patterns could be used to determine whether a teleme-

tered fish remained alive, emigrated, or died naturally, and that observed states for all individuals were determined without error. We assumed that all telemetered fish alive in the study area at time  $t$  were independent of each other and had the same transition and observation probabilities and survival rate to time  $t+1$ . Finally, telemetered and unmarked fish were also assumed to survive and emigrate at the same rates.

We used OpenBUGS software ([www.openbugs.info/w/](http://www.openbugs.info/w/); Lunn et al. 2009) to estimate  $t$ -specific instantaneous rates of  $E$ ,  $F$ , and  $M$ , discrete rates of overall fish survival (i.e.  $e^{-(F+M)}$ ), and  $p$  for spotted seatrout during the overwintering periods of 2009/2010 ( $t = 16$  wk), 2010/2011 ( $t = 5$  wk), and 2011/2012 ( $t = 31$  wk). Uninformative prior distributions were used for the natural logs of  $E$ ,  $F$ , and  $M$  [uniform  $(-10, 1)$ ], as well as for  $p$  [uniform  $(0, 1)$ ]. To estimate all parameter posterior distributions, we used 3 Markov chains of 17000 samples each but excluded the first 1000 samples of each chain in order to meet convergence criteria and to remove bias associated with initial parameter values. Convergence of the 3 Markov chains was assessed visually and confirmed based on the Brooks-Gelman-Rubin statistic ( $R < 1.05$ , McCarthy 2007). All parameter estimates are presented as posterior medians with a 95 % credible interval (CrI).

In order to directly identify a probable range of cold tolerance for spotted seatrout, we used a known-fates model with daily fate and temperature data from all years and study sites to estimate daily  $M$  for a total of 493 d. For this analysis, only telemetered fish passively or actively detected within the study areas on a given day were considered at risk; fish not detected at all or detected emigrating from a study site were not considered at risk. Also, we accounted for loss of fish from the daily at-risk pool due to inferred harvests. We modeled inferred natural deaths as a single (decreasing) logistic function of mean daily water temperature ( $^{\circ}\text{C}$ ) (see Supplement 2, [www.int-res.com/articles/suppl/m564p145\\_supp.pdf](http://www.int-res.com/articles/suppl/m564p145_supp.pdf)). For all  $M$  on day  $i$ :

$$M_i = 1 / \{1 + \exp[-(\beta_1 + \beta_2 T_i)]\} \quad (4)$$

where  $\beta_1$  is the intercept,  $\beta_2$  is the slope, and  $T_i$  is the mean water temperature recorded on a given day  $i$  for at-risk fish. We used OpenBUGS software to estimate model parameters and to predict daily  $M$  for the range in mean daily temperatures (i.e. 2 to 28 $^{\circ}\text{C}$ ) over which we observed telemetered spotted seatrout. Uninformative prior distributions were used for  $\beta_1$  and  $\beta_2$  [normal  $(0, 1.0e^6)$ ], and the natural log of  $F_i$  [uniform  $(-10, 1)$ ]. We estimated all parameter posterior distributions using 3 Markov chains of 55 000

samples each but excluded the first 5000 samples of each chain in order to meet convergence criteria and to remove bias associated with initial parameter values. Convergence of the 3 Markov chains was assessed as previously described and all parameter estimates are presented as posterior medians with a 95 % CrI.

## RESULTS

### Laboratory estimates of postsurgical survival and transmitter retention

Over 225 d of daily monitoring, we observed no postsurgical mortality for 8 spotted seatrout (mean  $\pm$  SE: 326.0  $\pm$  5.2 mm TL; 349.5  $\pm$  20.5 g WW; 3.1  $\pm$  0.2 % transmitter weight:fish weight) surgically implanted with dummy V13 transmitters or for 4 others (mean  $\pm$  SE: 427.0  $\pm$  11.3 mm TL; 797.5  $\pm$  42.7 g WW; 3.2  $\pm$  0.2 % transmitter weight:fish weight) receiving dummy V16 transmitters. During this 225 d experiment, mean water temperature was 13.4 $^{\circ}\text{C}$  (range: 4.7–28.5 $^{\circ}\text{C}$ ) and mean salinity was 30.6‰ (range: 27.8–33.7 ‰). A parasitic outbreak of the dinoflagellate *Amyloodinium ocellatum* began on Day 225 and resulted in mass mortality of both control and treatment fish, forcing termination of the experiment.

Necropsies of all fish performed at the termination of the experiment revealed that both control and telemetered fish were slightly emaciated. However, there was minimal evidence of deleterious effects (e.g. infection or necrosis) from the presence of a transmitter. Only 1 fish (349 mm TL) implanted with a V13 transmitter was judged by NCSU CVM staff to exhibit signs of infected and necrotic tissue, but this was only around the surgical wound. Transmitter retention was high, with only 1 telemetered spotted seatrout (317 mm TL) expelling the transmitter over the course of the retention experiment. This V13 transmitter loss occurred 40 d after surgery. Closer inspection revealed that the simple continuous suture knot loosened, resulting in complete unraveling of the sutures, dehiscence, and expulsion of the transmitter. This fish was not treated (i.e. the sutures were not repaired) but was closely monitored throughout the remainder of the experiment, during which it survived and the wound healed naturally. Therefore, we determined that V13-1H transmitters did not adversely affect the survival of spotted seatrout ( $\geq 356$  mm TL), nor did V16-4H transmitters in larger individuals ( $\geq 457$  mm TL). Although transmitter retention was high with simple continuous sutures, we suspected that it would be higher with

simple interrupted sutures. Consequently, simple interrupted suturing was used for all field surgeries where we assumed 100% retention.

**Temperature variability in North Carolina overwintering habitats**

Fine-scale (i.e. 15 min) measurements of water temperature were reduced to mean daily temperatures and the resulting long-term thermal profiles in each estuary were compared across telemetry seasons (Fig. 2). Low temperatures that were later confirmed in the laboratory to be lethal to spotted seatrout at either acute (3°C) or chronic (5°C) exposure (Anweiler et al. 2014, Ellis et al. in press) were reached in the Pungo River tributaries during the winters of 2009/2010 and 2010/2011 but not in 2011/2012. Tributaries of the Neuse River were only studied during the winter of 2011/2012 and did not experience lethal thermal conditions during that period. Thermal stress for spotted seatrout was apparently higher in the winter of 2010/2011 (CDD < 7°C = 144.3 d) than in the winter of 2009/2010 (CDD < 7°C = 80.4 d), and both winters were likely more stressful than the mild winter of 2011/2012 (Pungo River: CDD < 7°C = 0.6 d; Neuse River: CDD ≤ 7°C = 0.9 d).

**Interpretation and modeling analyses of telemetry data**

The daily movements and fates of 118 telemetered adult spotted seatrout were determined across 3 winters in North Carolina (Table 1). In the 2 study sites of the Pungo River, ultrasonic transmitters were surgically implanted in 37 spotted sea-

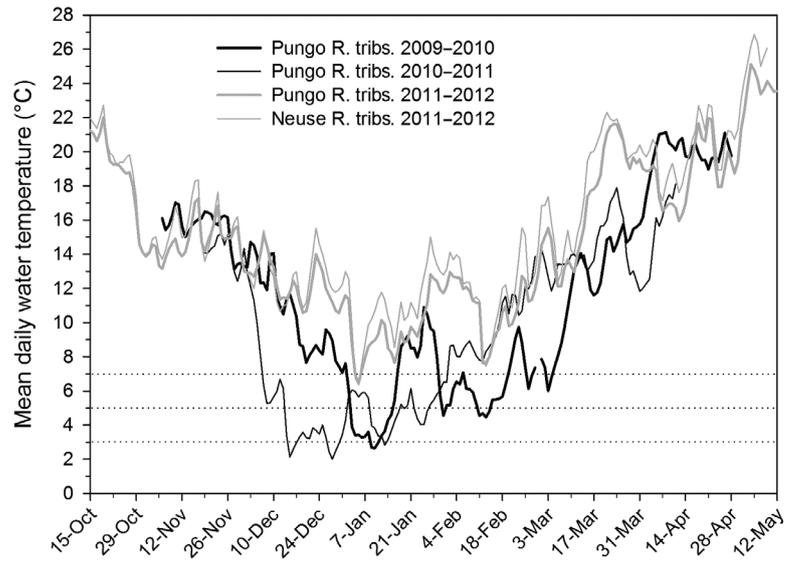


Fig. 2. Mean daily water temperature observed in study tributaries of the Pungo River estuary (2009/2010, 2010/2011, and 2011/2012) and Neuse River estuary (2011/2012) in North Carolina, USA; temperature measurements taken at a uniform depth of ~1.5 m in each estuary. References (dotted lines) to low temperature treatments that affected survival under controlled laboratory conditions (see Ellis et al. in press) are also presented

Table 1. Summary of telemetry study results including the number of fish tagged and released, range of total length, range of days at risk, beginning and end dates of daily data availability, and assumed fates for telemetered spotted seatrout that were tracked during 3 consecutive winters in 2 adjacent tributaries of the Pungo River and during 1 winter in 2 adjacent tributaries of the Neuse River, North Carolina, USA. Number of individuals for a given fate is presented with the proportion of the total number tagged (in parentheses) for that winter and river system

Telemetry study results	Pungo R.			Neuse R.
	2009/2010	2010/2011	2011/2012	2011/2012
Number tagged	37	10	26	45
Total length (mm, range)	372–502	360–440	361–495	362–540
Days at risk (range)	7–101	3–22	11–173	2–172
Date of first fish release (mo/d)	12/01	11/18	11/02	11/07
Date of last fish at risk (mo/d)	03/18	12/16	05/30	05/22
Surgery-related mortality	0	1 (0.10)	0	0
Permanent emigration within 7 d	3 (0.08)	0	2 (0.08)	3 (0.07)
Fishing mortality				
Total	1 (0.03)	0	4 (0.15)	4 (0.09)
Confirmed	0	0	0	4 (0.09) <sup>a</sup>
Unconfirmed	1 (0.03)	0	4 (0.15)	0
Natural mortality				
Total	7 (0.19)	6 (0.60)	1 (0.04)	0
Stationary transmitter	2 (0.05)	5 (0.50)	0	0
Removal during cold episodes	5 (0.14)	1 (0.10)	0	0
Inferred predation event	0	0	1 (0.04)	0
Emigration after 7 d	26 (0.70)	3 (0.30)	19 (0.73)	38 (0.84)

<sup>a</sup>One of these 4 confirmed fishing mortalities occurred during a 7 d censorship period (see 'Materials and methods'); proportion is of total number tagged

trout (mean  $\pm$  SE: 430.1  $\pm$  4.7 mm TL; 741.3  $\pm$  24.9 g WW; 1.5  $\pm$  0.1% transmitter weight:fish weight) during winter 2009/2010, 10 spotted seatrout (mean  $\pm$  SE: 379.6  $\pm$  8.2 mm TL; 500.5  $\pm$  45.9 g WW; 2.2  $\pm$  0.2% transmitter weight:fish weight) during winter 2010/2011, and 26 spotted seatrout (mean  $\pm$  SE: 414.7  $\pm$  8.1 mm TL; 735.9  $\pm$  43.2 g WW; 1.6  $\pm$  0.1% transmitter weight:fish weight) during winter 2011/2012. In the 2 study sites of the Neuse River, 45 spotted seatrout (mean  $\pm$  SE: 460.0  $\pm$  7.1 mm TL; 965.3  $\pm$  42.6 g WW; 1.5  $\pm$  0.1% transmitter weight: fish weight) were surgically implanted with ultrasonic transmitters during winter 2011/2012. During all 3 telemetry study periods and in all study sites, VR2/W receivers logged a combined 2 294 598 detections from all 118 telemetered spotted seatrout. Manual relocation percentages of telemetered fish were also high during all 3 telemetry study periods. Thirty-four of 37 (92%) telemetered spotted seatrout were manually tracked in 2009/2010, 10 of 10 (100%) in 2010/2011, and 64 of 71 (90%) in 2011/2012.

Ten fish were excluded from our modeling analyses due to an inferred surgery death ( $n = 1$ ), permanent emigration ( $n = 8$ ), or a confirmed fishing mortality (i.e. transmitter was returned by fisher;  $n = 1$ ) during a 7 d censorship period (Table 1). For the remaining at-risk telemetered spotted seatrout ( $n = 108$ ), and beginning on the first day after the 7 d censorship period, the mean ( $\pm$  SE) days-at-risk in the Pungo River tributaries were 52.7  $\pm$  3.8 for the 2009/2010 telemetry period, 11.1  $\pm$  2.1 for 2010/2011, and 90.8  $\pm$  8.0 for 2011/2012, and 97.7  $\pm$  5.7 in the Neuse River tributaries for the 2011/2012 telemetry period. Overall, fates inferred from the movements of these at-risk fish included harvest (confirmed from fisher return of acoustic transmitter,  $n = 3$ ; unconfirmed,  $n = 5$ ), natural mortality ( $n = 14$ ), and permanent emigration ( $n = 86$ ) (Table 1).

During the 2009/2010 telemetry period in the Pungo River, there was 1 unconfirmed harvest and 7 assumed natural deaths (Table 1, Fig. S1 in Supplement 3, [www.int-res.com/articles/suppl/m564p145\\_supp.pdf](http://www.int-res.com/articles/suppl/m564p145_supp.pdf)). Two of the 7 assumed natural mortalities were judged based on a lack of transmitter movement and the other 5 based on permanent loss of transmitter signal during cold episodes (i.e. scavenger removal or hand harvest of cold-stunned fish). Multistate models of telemetry data performed poorly (e.g. nonsensical parameter estimation) when sample sizes were low. Therefore, we limited our analyses of modeling results for each overwintering period to weeks when  $\geq 10$  telemetered spotted seatrout were at risk. Across 11 wk, from 8 December

2009 to 21 February 2010, detection probability was high, with estimated weekly  $p_t$  ranging from 0.915 (CrI: 0.784, 0.980) to 0.980 (CrI: 0.899, 0.999). Weekly estimates of  $E_t$  ranged from 0.001 (CrI: 0, 0.039) to 0.517 (CrI: 0.178, 1.164), increased with the onset of extreme low temperatures in early January, and were highest in mid-February (Fig. 3A). Weekly mortality rates were constant and relatively low until February (Fig. 3B,C). Estimates of  $F_t$  ranged from 0.001 (CrI: 0, 0.038) to 0.002 (CrI: 0, 0.126) and were similar or lower than estimates of  $M_t$ , which ranged from 0.001 (CrI: 0, 0.039) to 0.187 (CrI: 0.027, 0.625). The low precision of these parameter estimates, especially during periods of high emigration and high natural mortality, was likely due to the smaller sample size of telemetered spotted seatrout that were at risk (Fig. 3D). Total weekly fish survival ranged from 0.817 (CrI: 0.521, 0.968) to 0.996 (CrI: 0.943, 1) (Fig. 3E). Reduced survival, almost entirely due to  $M$ , was estimated either during or immediately following when mean weekly temperatures were  $< 5^\circ\text{C}$ . However, estimated survival was high in January 2010 when temperatures dropped below  $4^\circ\text{C}$ . Coincidentally, most telemetered spotted seatrout that were at risk during these 2 weeks remained undetected (primarily by stationary VR2/W receivers) for several consecutive days, indicating that movement rates were low and fish were occupying unmonitored habitats (Fig. S1 in Supplement 3).

There was no presumed harvest of telemetered spotted seatrout during the 2010/2011 telemetry period in the Pungo River tributaries. We inferred that 6 of 9 at-risk fish died naturally, based on either a lack of movement ( $n = 5$ ) or a permanent loss of transmitter signal during low temperatures ( $n = 1$ ) (Table 1, Fig. S2 in Supplement 3). More specifically, 5 of 9 fish emigrated from the study sites in early- to mid-December 2010, likely in response to a rapid decline in water temperature. Two of these individuals returned days later, and all 6 fish at risk died during a 2 d period when mean daily temperatures were  $< 3^\circ\text{C}$  (Figs. 2 & S2). Due to the low sample size of telemetered spotted seatrout at risk (i.e.  $< 10$  fish), data collected during the 2010/2011 telemetry period were insufficient for multistate modeling. However, these data were included in our daily survival model where we used logistic regression to predict daily  $M$  as a function of mean daily water temperature (see below, this sub-section), and the estimates of daily  $M$  when temperature was  $\leq 3^\circ\text{C}$  were largely based on the natural deaths of these 6 spotted seatrout.

Tributaries of 2 separate estuarine systems were studied during the overwinter telemetry period of

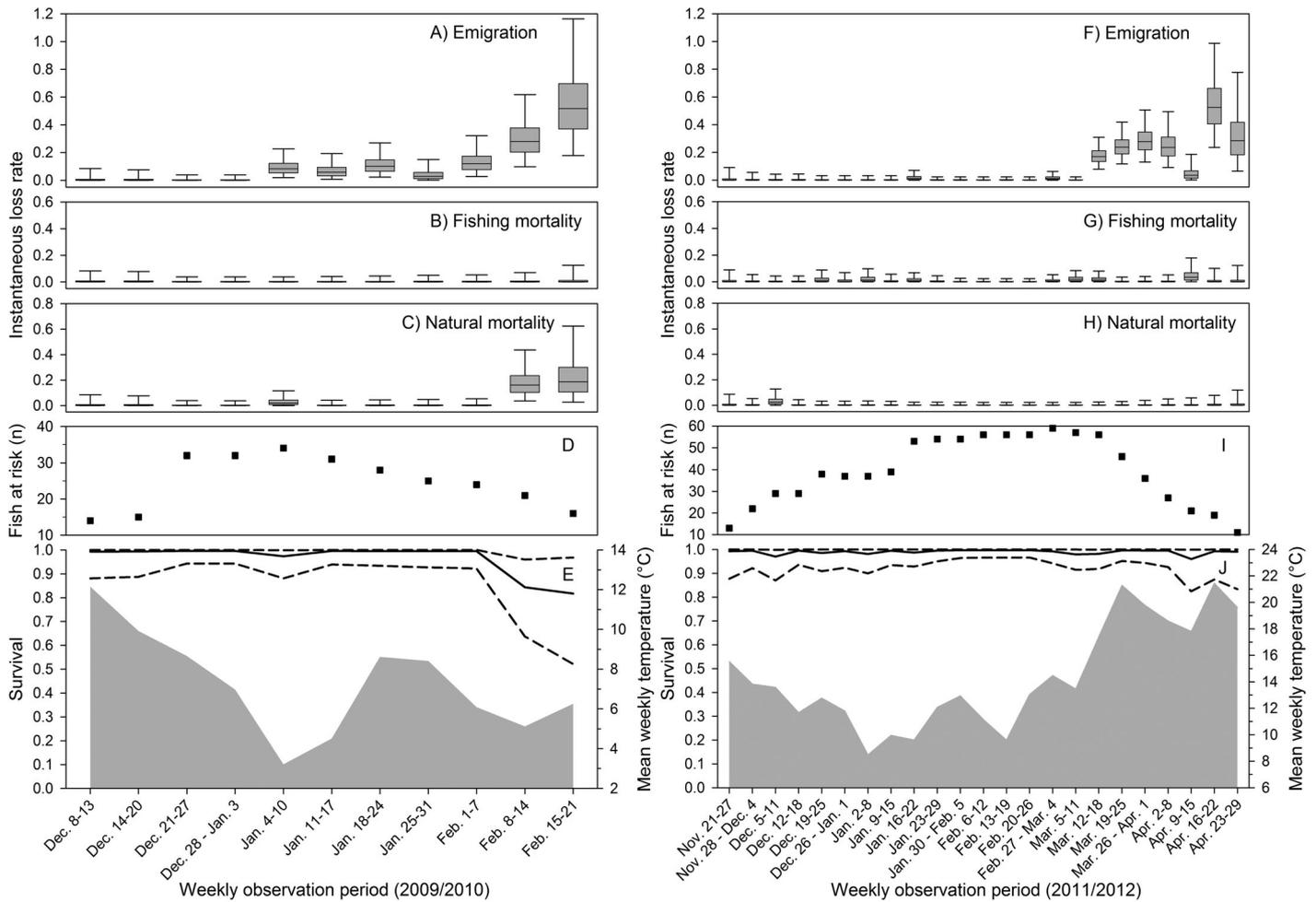


Fig. 3. Box-and-whisker plots of instantaneous rates of emigration, fishing mortality, and natural mortality across (A–C) 11 weekly observation periods (December 2009 to February 2010) in 2 tributaries of the Pungo River, North Carolina, USA, and (F–H) 23 weekly observation periods (November 2011 to April 2012) in 2 tributaries of the Pungo River and 2 tributaries of the Neuse River, North Carolina, USA. Shaded box: interquartile range (IQR); top and bottom of box: 75th and 25th percentiles, respectively; horizontal line: median; whiskers: 95% credible interval (i.e. the 97.5th and 2.5th percentiles). (D,I) Number of fish at risk (only estimates for weeks with  $\geq 10$  fish are shown). (E,J) Estimated overall survival (median  $\pm$  95% credible interval) relative to mean weekly water temperature (shading; averaged across both river estuaries in [J])

2011/2012. Of the 24 fish at risk in the Pungo River tributaries, there were 4 unconfirmed harvests, and of the 41 fish at risk in the Neuse River tributaries, there were 4 confirmed harvests (Table 1, Fig. S3 in Supplement 3). Although no cold-induced natural mortality was observed during this telemetry period, we inferred that a possible predation event occurred for 1 telemetered spotted seatrout in the Pungo River study system (see results for emigration speeds below). As such, we assigned a fate of natural mortality for this fish in our multistate model. Given the overall similarities in numbers and types of mortalities, timing of emigration events, and days at risk for telemetered spotted seatrout in tributaries of the Pungo and Neuse Rivers (Table 1, Fig. S3), we com-

bined data across river estuaries for multistate modeling analysis to permit greater precision of parameter estimates. Across 23 wk, from 21 November 2011 to 29 April 2012, detection probability was high, with estimated  $p_t$  ranging from 0.560 (CrI: 0.402, 0.709) to 0.982 (CrI: 0.907, 0.999). Estimated  $E_t$  ranged from 0.001 (CrI: 0, 0.023) to 0.524 (CrI: 0.236, 0.988), increased rapidly in mid-March, and was highest in mid-April (Fig. 3F). Weekly instantaneous mortality rates were consistently low, including  $M_t$ , which was only observed once (Fig. 3G,H). Estimates of  $F_t$  ranged from 0.001 (CrI: 0, 0.023) to 0.033 (CrI: 0.001, 0.179) and were similar to  $M_t$ , which ranged from 0.001 (CrI: 0, 0.023) to 0.024 (CrI: 0.001, 0.128). Again, the low precision of some parameter esti-

mates, especially during periods of high emigration, was likely due to the smaller sample size of telemetered spotted seatrout that were at risk (Fig. 3I). In contrast to the previous 2 winters, water temperatures during the winter of 2011/2012 in the Pungo River, as well as in the Neuse River, never reached the laboratory-derived critical lows of 3 and 5°C, and total weekly survival of spotted seatrout across both study sites was high over the 6 mo telemetry period, ranging from 0.960 (CrI: 0.824, 0.998) to 0.997 (CrI: 0.966, 1) (Fig. 3J).

Estimates of emigration swimming speeds of telemetered spotted seatrout ranged from 0.1 to 7.9 km h<sup>-1</sup> (mean ± SE: 0.624 ± 0.094). Over the combined duration of our telemetry study, we observed the presence of bottlenose dolphins in our study systems on only 4 of 98 (4%) field days, and were able to estimate swimming speeds (5.1 km h<sup>-1</sup>) for 1 of those days. All but 1 telemetered spotted seatrout (i.e. 98.9% of emigrating transmitters) had estimated swimming speeds well below our single estimate and the estimates reported by Bachelier et al. (2009) for bottlenose dolphins from the same or similar estuarine tributaries (Fig. S4 in Supplement 4, [www.int-res.com/articles/suppl/m564p145\\_supp.pdf](http://www.int-res.com/articles/suppl/m564p145_supp.pdf)). Although apparently rare in our study, it appears that a single predation event by a bottlenose dolphin occurred, given the atypically high speed (7.9 km h<sup>-1</sup>) at which this transmitter emigrated from Pantego Creek on 8 December 2011.

From our daily survival model, the logistic function relating mean daily water temperature to daily  $M$  for all years and all study sites combined predicted that

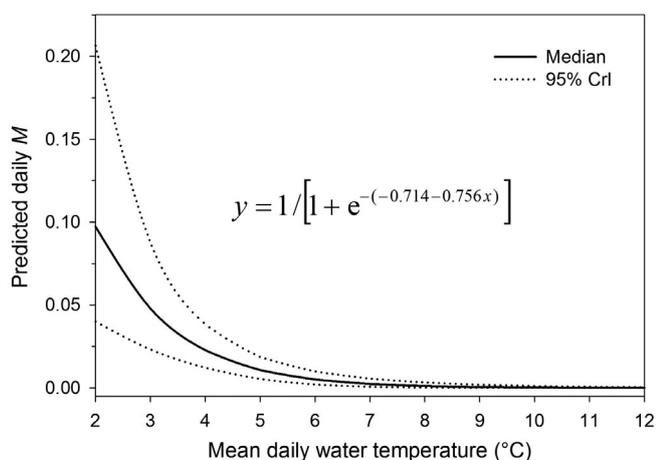


Fig. 4. Logistic regression of instantaneous daily natural mortality rate ( $M$ ) for spotted seatrout as a function of mean daily water temperature. Daily estimates of  $M$  were derived from a known-fates model of telemetered fish whose daily movements were tracked in major tributaries of the Pungo and Neuse Rivers, North Carolina, USA, and across 3 winter study periods from 2009 to 2012. CrI: credible interval

daily  $M$  was elevated at temperatures <~7°C (Fig. 4). The intercept ( $\beta_1$ ) of the logistic function was estimated to be -0.714 (CrI: -2.133, 0.795) and the slope ( $\beta_2$ ) was estimated to be -0.756 (CrI: -1.113, -0.487), which correspond to a precipitous increase in the predicted daily  $M$  at temperatures <~4°C. Estimates of precision decreased as temperature decreased due to the relatively few fish at risk, especially as temperatures reached apparently stressful levels (i.e. ≤5°C). Thus, spotted seatrout are susceptible to cold-induced mortality at water temperatures <7°C.

## DISCUSSION

Estimates of mortality from winterkill in adult fishes are rare because of the episodic nature of severe winter conditions and the difficulty in estimating mortality *in situ*. The acoustic telemetry approach used in this study allowed for direct measurement of spotted seatrout mortality in, and emigration from, North Carolina overwintering habitats. Natural mortality of spotted seatrout was high during winters when declines in water temperature below 7°C were severe (CDD < 7°C = ~80 to 144 d). The winterkill of telemetered fish that we observed in the 2009/2010 and 2010/2011 study periods, corroborates tag-return estimates of mortality for spotted seatrout in North Carolina and Virginia, where estimates of  $M$  were highest for those same winters throughout a 4 yr time series (Ellis 2014). Natural mortality was not observed in either the Pungo River or Neuse River study sites during the 2011/2012 telemetry period when temperatures were mild (CDD < 7°C = ~1 d), which coincides with low estimates of winter  $M$  from conventional tagging (Ellis 2014). Severity of winter has been related to low winter survival using either indirect (e.g. pre- and post-winter changes in size distributions and abundance; Hurst & Conover 1998, Hare & Able 2007) or more direct (e.g. tagging estimates of winter mortality; Adams et al. 2012, Barbour et al. 2014) approaches, but none of these approaches allow the direct linkage between daily temperatures and a mortality estimate as we have demonstrated here.

Previous reports of winterkill suggest anecdotally that lethal thermal conditions for spotted seatrout begin at water temperatures ranging from 3 to 10°C (Gunter & Hildebrand 1951, Moore 1976, Gilmore et al. 1978, McEachron et al. 1994). In general, our direct observations suggest that when water temperatures at depths of 1.5 m fell below 5 to 7°C, telemetered spotted seatrout responded by either emigrat-

ing from the study sites, by occupying unmonitored habitats within the study sites that were likely in deeper, warmer water (i.e. > 1.5 m), or by remaining in the relatively shallow habitats at ~1.5 m. In the latter case, our data provide strong evidence of spotted seatrout mortality due to acute cold stress. Furthermore, sustained temperatures in the range of 8 to 10°C during the 2011/2012 study period, with no temperatures <6°C recorded, were not lethal to telemetered spotted seatrout. During the 2010/2011 winter, our telemetry tagging ended earlier than expected because of an unusual early and prolonged cold period in December 2010 (i.e. fish were no longer vulnerable to angling). Thus, few fish were tagged with ultrasonic transmitters prior to the onset of these extreme cold conditions. Although this low sample size would be expected to decrease the likelihood of observing natural mortality, and was insufficient for multistate modeling,  $M$  was likely extremely high during this winter, since all 6 telemetered spotted seatrout that were at risk (i.e. did not emigrate) were inferred to have died due to cold temperatures based on their movement patterns. We also found many moribund and dead spotted seatrout floating at our study sites ( $n = 198$ , TL range: 256–627 mm; T. Ellis unpubl. data) while conducting a manual search for telemetered fish over ~10 h on January 5, 2011, which provides further support for high  $M$  during the 2010/2011 winter. The majority of these dead fish were in various stages of decomposition, indicating that the mass mortality event likely occurred during the previous week when ice cover prevented complete manual searches of our study sites on December 29, 2010. Floating spotted seatrout ( $n = 12$ ) were also observed in our study sites during the 2009/2010 winter over multiple days of manual searches (coinciding with increases in our estimates of  $M$  during this winter) but not during any manual search conducted during the 2011/2012 winter.

All rapid-onset-of-cold events that resulted in winterkill of telemetered spotted seatrout involved water temperatures <7°C. The species' probable range of cold intolerance (i.e. mean daily water temperature <~7°C with a precipitous increase in predicted daily  $M$  at temperatures <~4°C) that we identified through *in situ* observations of telemetered fish is supported by results obtained under controlled experimental conditions (see Anweiler et al. 2014, Ellis et al. in press). Both of these laboratory assessments suggest that when exposed to temperatures at or below ~4°C, spotted seatrout undergo the physiologically-limiting effects of acute cold stress. Ellis et al. (in press) also found that while survival of 10 d exposure to 7°C was

high in the laboratory, it was not absolute (~83%). In the present study, winterkill was observed in both the 2009/2010 and 2010/2011 telemetry periods when temperatures <7°C persisted for ≥10 d.

The low number of inferred harvests of telemetered spotted seatrout in our study sites for all 3 separate telemetry study periods was unexpected considering the popularity of these estuarine tributaries among recreational anglers and the high level of fishing effort we regularly observed during manual tracking events. In all 4 study sites, we often relocated the acoustic signal of telemetered fish in the immediate vicinity of anglers, and stationary receivers recorded telemetered fish successfully avoiding commercial gill nets set in lower Pungo Creek. Although fishing mortality is not the emphasis of this paper, it had to be estimated concurrently with natural mortality, as both are competing sources of mortality.

Similarly, our multistate model also accounted for the loss of telemetered fish due to emigration. The timing of the mass emigration of at-risk telemetered fish that we observed across all 4 study sites during the latter half of March 2012 is consistent with what is known about the reproductive condition and onset of spawning behavior for spotted seatrout in North Carolina (NCDMF 2012) and areas south (Brown-Peterson 2003, Lowerre-Barbieri et al. 2009). Deeper and higher-salinity portions of the lower estuary are utilized by spotted seatrout in North Carolina during a protracted (~6 mo) summer spawning season (Luczkovich et al. 2008). During this time, spotted seatrout are largely absent from the relatively shallow, lower-salinity tributaries of the upper estuary that we studied. Such differential use of the estuary by adult spotted seatrout (upper portion in winter versus lower portion in summer) has been reported for more southerly-distributed populations as well (Baker et al. 1986, Woodward et al. 1990, Helser et al. 1993, Wenner & Archambault 1996). Similar to North Carolina, spotted seatrout are found in a variety of habitats during the summer spawning season in estuaries to the south, including over soft bottom, vegetated, and shell-dominated substrates (Brown-Peterson 2003, Lowerre-Barbieri et al. 2009, Walters et al. 2009, Lowerre-Barbieri et al. 2013). Strong associations with seagrass habitat, current velocity, and physicochemical variables (temperature, salinity, and dissolved oxygen) suggest that spawning spotted seatrout may aggregate in areas where environmental conditions optimize the dispersal, growth, and survival of early life-history stages (Peebles & Tolley 1988, Saucier & Baltz 1993, Walters et al. 2009).

We are unaware of any empirical data regarding this species' habitat requirements during winter. However, anecdotal reports of winterkill suggest that the availability of thermal refuge, as proximity to either coastal inlets or deeper channels, is the most important factor influencing spotted seatrout survival during an extreme cold event (Pearson 1928, Moody 1950, Gunter & Hildebrand 1951, Tabb 1966, Moore 1976). Others have described the importance of thermal refuges to fishes overwintering in estuaries (Smith & Able 1994, Hanson & Courtenay 1996, Barbour et al. 2014, Tomie et al. 2017). Although our study sites were located considerable distances (>75 km) from ocean access, observations during our study provide support for the understanding that deeper habitats can serve as thermal refuges. A clear example of this was when both passive and active telemetry tracking missed most at-risk individuals during the extreme cold event that lasted throughout most of January 2010. Survival of telemetered spotted seatrout during this time — when temperatures at depths of 1.5 m were <4°C and deemed lethal — was most likely the result of behavioral thermoregulation (i.e. movement from monitored to unmonitored habitats of apparently warmer water). In subsequent years of our study, we identified new potential refuge habitats in Pungo Creek by conducting manual searches further upstream and finding high concentrations of telemetered fish in these previously unmonitored deeper (i.e. > 1.5 m) and likely warmer habitats. Similarly, the emigrations observed from the Pungo River study sites in February 2010 appear to have been influenced by weather that resulted in not only extreme cold (i.e. < 7°C) but also low water (due to strong westerly winds), which potentially affected the accessibility and availability of refuge habitat within the study area. High winds can alter current direction and velocity, increasing energy demand (i.e. swimming activity) necessary for locating or occupying thermal refuges. More importantly, and as was suggested for a cold-kill event in Florida, high winds can lead to a greater mixing of the water column that can eliminate the critical thermoclines that allow for effective winter refuge habitat (Gilmore et al. 1978). Our results confirm that these emigrations from our study sites were permanent but the fate of telemetered spotted seatrout outside of these areas is unknown. During both of these winter time periods, high estimates of  $M$  from a separate statewide tag-return study (Ellis 2014) suggest that telemetered spotted seatrout were unlikely to find thermal refuge by leaving our study sites during cold conditions.

The winter ecology of spotted seatrout should be studied in other portions of its geographic range in order to better understand why this species in North Carolina and elsewhere (e.g. Chesapeake Bay) historically overwinter in habitats susceptible to cold-kill conditions. Undoubtedly, such a risk must be outweighed by one or more important ecological benefits. The seasonal egress of several other temperate estuarine-dependent fishes from shallow estuaries as temperatures decline (Able et al. 2014) suggests that spotted seatrout may be unique in regards to utilization of the upper estuary as overwintering habitat. Our results provide evidence of low natural mortality for spotted seatrout during mild winters in lower-salinity estuarine habitats, but it is unknown what environmental factors (abiotic and biotic) influence this species' use of the upper estuary during winter. Survival of other euryhaline species at low temperatures has been shown to be highest under presumed isosmotic conditions (Prentice 1989, Lankford & Targett 2001, Hurst & Conover 2002), which for spotted seatrout (see Wohlschlag & Wakeman 1978) are likely the mesohaline regions typical of the upper estuary. However, Ellis et al. (in press) found no measured effect of salinity on spotted seatrout survival to prolonged exposure to cold. Tabb (1958) postulated that the euryhalinity of spotted seatrout has allowed the species to occupy the lower-salinity environments of the upper estuary that typically have abundant prey and limited competition for resources. The seasonal movement of bottlenose dolphins from Pamlico Sound to the coastal waters of North Carolina during winter (Goodman Hall et al. 2013) may also result in a lower risk of predation for spotted seatrout in this region overwintering in the upper estuary. The behavioral responses of spotted seatrout relative to environmental change (abiotic and biotic) that influence distribution, habitat utilization, residency, and survival, are important areas for future study.

#### **Additional assumptions and potential biases**

The assumptions of the multistate model and several key assumptions regarding fate assignments were listed in 'Materials and methods'. Additional assumptions and potential biases that relate to our telemetry approach for estimating mortality are discussed here.

Natural mortality inferred from stationary transmitters and manual searches could be misinterpreted if telemetered fish experienced discard mortality (i.e. death associated with a recreational or commercial

catch and release: Hightower & Pollock 2013). We found no indication that discard mortality of telemetered spotted seatrout caught and released by recreational and commercial fishers biased the weekly estimates of  $F$  and  $M$  in our study. The majority of natural mortalities based on a stationary transmitter (6 of 7; 86%), occurred during extreme cold conditions when observed fishing effort was nearly nonexistent. Furthermore, though the majority of inferred harvests in our study (8 of 9; 89%) occurred during the 2011/2012 telemetry period, we observed no stationary transmitters during that time, meaning that there were no possible misinterpretations of fate (e.g. catch-and-release mortality).

Similarly, repeated relocation of a transmitter signal in a constant position could result from fish expulsion of the transmitter while in the study area. The results of our long-term captive study and the high tag-retention rates apparent in our field study and other field studies (Callihan et al. 2013, Lowerre-Barbieri et al. 2013) suggest the potential for this bias was low.

If a transmitter failed prematurely, this would be misinterpreted as a harvest. While there is no precise way to assess transmitter failure beyond ensuring full transmitter functionality prior to releasing a telemetered fish, the likelihood of this bias in our study was small given that transmitters from all stationary natural and surgery-related mortalities (V13-1H,  $n = 8$ ) continued to transmit throughout the manufacturer-guaranteed battery life.

Estimation of survival from acoustic telemetry requires objective criteria for determining if a predator consumed or if a fisher removed a telemetered fish (Heupel & Simpfendorfer 2002, Bacheler et al. 2009, Gibson et al. 2015). Our data suggest that predation on telemetered spotted seatrout in our study sites was low. We inferred that the loss of transmitter signal for 6 fish during extreme cold events was due to either the opportunistic predation from birds on or the removal (i.e. dip netting) by fishers of lethargic spotted seatrout (a fishing technique that we observed during cold-stun events). Both of these scenarios are a direct consequence of acute cold stress and were most appropriately assigned as natural mortality. However, during all other times (i.e. water temperatures  $\geq 7^{\circ}\text{C}$ ) we showed through estimated emigration swimming speeds that negative bias in our estimates of  $M$  due to unaccounted-for predation by bottlenose dolphins was minimal. In only 1 of 95 (1%) permanent emigration events did the speed of a transmitter passing through our receiver array overlap with the reported speeds of bottlenose dolphins. The use of swimming

speed has proven effective in separating out predation events for juvenile sharks (Heupel & Simpfendorfer 2002), subadult red drum (Bacheler et al. 2009), and Atlantic salmon smolts (Gibson et al. 2015) in other estuarine telemetry studies.

Variability in environmental parameters (e.g. wind speed) affect detection probabilities for telemetered fish (Kessel et al. 2014). The placement of our stationary receivers resulted in high overlap of detection ranges, which reduced the potential for environmental parameters to prevent us from detecting telemetered fish leaving the study system. A high density of stationary receivers, along with frequent manual tracking, resulted in high weekly estimates of detection probability, which provide confidence in our fate assignments for telemetered spotted seatrout.

### Future considerations and conclusions

Acoustic telemetry can be an effective method for direct estimation of fish mortality in open, dynamic ecosystems, including estuaries, given that there are no adverse effects of the methodology on the species of interest that can bias study results. Specifically, the surgical implantation of an ultrasonic transmitter should not limit long-term survival or alter normal behavior of the telemetered fish (Bridger & Booth 2003). Transmitter retention must also be absolute for the duration of the study (i.e. transmitter battery life). Reese Robillard et al. (2015) reported relatively high rates of tagging-induced mortality (26%) and transmitter loss (18% with monofilament sutures) for spotted seatrout, but acknowledged that the additional placement of an internal anchor tag in the incision may have biased their results. The authors of that laboratory study also did not anesthetize experimental fish, and found surgery time to be a significant predictor of postsurgical survival. The much higher rates of postsurgical survival and tag retention in our laboratory and field study and that of Callihan et al. (2013) and Lowerre-Barbieri et al. (2013) suggest that sedation with no internal anchor tag placed within the incision should be a best practice for surgically implanting transmitters in this species.

Our telemetry approach provided reliable *in situ* estimates of the mortality of spotted seatrout relative to acute cold stress. Nevertheless, our real-time monitoring of temperature at only 1 or 2 stationary receivers per study site was likely an incomplete record of the thermal history experienced by each telemetered spotted seatrout. We recommend that future studies increase the spatial coverage of environmen-

tal monitoring, particularly in areas that may provide refuge from environmental stressors. However, identifying potential refuge habitat can be difficult, especially in larger systems, and will require not only detailed habitat mapping but also a strong understanding of the relationship between the physical habitat and the abiotic environment. An alternative approach for linking environment to fish movement and mortality would be the use of ultrasonic tags with data sensors (see review by Cooke et al. 2012), which would be a significant advantage over our telemetry approach, especially given the variability in thermal conditions observed in our estuarine study sites. Despite the main advantage of providing environmental data (e.g. temperature and depth) at the individual level, ultrasonic tags with sensor capabilities are substantially more expensive, which may limit their use in studies with budgetary constraints, such as studies where a considerable number of telemetered fish are needed for reliable estimates of mortality rates. Due to the schooling behavior of telemetered spotted seatrout that we observed in our study sites during winter, using a mix of temperature-sensing and non-sensor ultrasonic tags may provide more direct information than stationary temperature loggers regarding the thermal environment experienced by the majority of telemetered fish, while still meeting minimum sample size objectives necessary for survival estimation.

Effective management of this valuable fishery resource requires an accurate understanding of the relative importance of winterkill on spotted seatrout population dynamics. In temperate latitudes, variability in and vulnerability to abiotic factors, particularly temperature, are considered highest at the edges of a species' geographic range (Miller et al. 1991, Myers 1998). Our results give new insight into the winter ecology of spotted seatrout through evidence that acute cold stress can be a major driver of overwinter loss for this species at its northern latitudinal limits. Furthermore, these are the first direct field-based estimates of  $M$  for spotted seatrout, and are much improved over the general life-history relationships based on weight and longevity (e.g. Hoenig 1983, Lorenzen 1996) that typically serve as proxies for  $M$  in stock assessments for this species. We highly recommend our telemetry approach to link fine temporal scale measurements of mortality and environmental stressors in other fishes.

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