Estimating Fish Mortality Rates Using Telemetry and Multistate Models

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We simulated and evaluated multistate capture-recapture models to estimate mortality rates using telemetry data. Four field designs were considered: (A) fixed receivers to estimate total instantaneous mortality (Z), (B) manual searches to estimate instantaneous fishing (F) and natural (M) mortality, (C) fixed receivers combined with external high-reward tags to estimate F and M, and (D) manual searches combined with external high-reward tags to estimate M and fishing mortality rates associated with harvest (Fh) and catch-and-release death (Fa) as well as the probability of death due to catch and release (α). Estimates generally appeared to be unbiased for a simulated study with five periods and releases of telemetered fish at the start of periods 1–4. Compared to estimating Z, larger sample sizes are needed to achieve reliable estimates of component rates (F and M). Estimates of component rates were more precise when that source of mortality was directly observed (M in design B, F in design C). The field design using fixed receivers and high-reward tags should be especially useful in practice, because manual searches are not required to estimate F and M. Multistate models are useful for clarifying the connection between field observations and ecological processes. Reliable estimates of mortality rates, coupled with information on behavior, habitat use, and movement, make telemetry a highly valuable tool for improving fisheries management and stock assessment.

INTRODUCTION

Reliable information about fish mortality rates is essential for stock assessment, effective management of fisheries, and recovery of rare or declining populations. A useful starting point may be to estimate the total rate of mortality due to all sources, for example, by a catch curve analysis (Ricker 1975) or a tag-return study (Brownie et al. 1985). However, especially for harvested populations, an estimate of the total rate of mortality may not meet management objectives. More information is often needed, such as mortality due to fishing (e.g., recreational, commercial, or catch and release), habitat (e.g., barrier passage or areas with poor water quality), and natural causes (e.g., predation or spawning behavior). Fishing mortality can be investigated by monitoring fishing using traditional stock assessment methods, although these methods generally require many years of fishery and survey data to obtain reliable estimates (Hilborn and Walters 1992). Fishing mortality can also be estimated from fishery tag returns (Brownie et al. 1985; Hoening et al. 1998) as long as tag reporting rates can be accurately estimated (Pollock et al. 1991). Other sources, however, such as natural mortality, are often more difficult to assess directly. For stock assessment, natural mortality is usually an assumed value based on life history characteristics such as maximum age, body size, or growth (Pauly 1980; Lorentzen 1996; Then et al. 2015). Assumed rates may capture broad life history trends (e.g., higher natural mortality for smaller or short-lived species) but do not account for species differences; characterize local or temporal effects due to habitat quality, predator abundance, or seasonal behavior; or assess the magnitude of different sources such as from birds, fish, and sea lions, for example (Hollowed et al. 2000; Keefer et al. 2012; Hostetter et al. 2015). Accurate and precise estimates of component mortality rates are often essential for successful fisheries management (e.g., Hewitt et al. 2007). One effective approach for estimating multiple mortality rates for a fish population is through the use of telemetry. Telemetry facilitates the simultaneous study of fish movement and mortality rates (Jepsen et al. 1998; Hightower et al. 2001), thus enabling temporal (Waters et al. 2005) and spatial (Gardner et al. 2010; McMichael et al. 2010) estimates of total mortality or multiple components of mortality, depending on study design and analysis. Technological advances have resulted in transmitters that can be tracked out of water and related to predator signs such as tracks, droppings, hair, or proximity to a den. PIT tags, which can be detected using fixed arrays (Hewitt et al. 2010; Barbour et al. 2012; Haesecker et al. 2012) or portable antennas (in small streams; Fetherman et al. 2014), are small and relatively inexpensive, making them a good approach for identifying components of natural mortality, especially for small fish (Hostetter et al. 2015).

METHODS

Telemetry Tag Type

The field designs we evaluate work with sonic or radio telemetry or even passive integrated transponder (PIT) tags. Sonic telemetry can be used in freshwater or saltwater systems and sonic receiver arrays are increasingly common in coastal and marine waters (Heupel et al. 2006; McMichael et al. 2010). Radio telemetry is limited to freshwater systems but may be preferred in shallow areas or where vegetation or noise (e.g., turbulence around a dam) could limit the effectiveness of sonic equipment (Cooke et al. 2012). Radio transmitters are valuable for detecting mortality by terrestrial predators (Muhametsazina et al. 2014) because tags can be tracked out of water and related to predator signs such as tracks, droppings, hair, or proximity to a den. PIT tags, which can be detected using fixed arrays (Hewitt et al. 2010; Barbour et al. 2012; Haesecker et al. 2012) or portable antennas (in small streams; Fetherman et al. 2014), are small and relatively inexpensive, making them a good approach for identifying components of natural mortality, especially for small fish (Hostetter et al. 2015).

Study Design

Four study designs are considered here: (A) fixed receivers, telemetry only: to estimate total instantaneous mortality (Z); (B) manual searches, telemetry only, which could be augmented by fixed receivers: to estimate instantaneous fishing (F) and natural (M) mortality rates; (C) fixed receivers, telemetry with external tag return, direct estimation of multiple spatial and temporal fishing and natural mortality rates is possible. Bayesian analysis using flexible open-source software such as JAGS (Plummer 2003) has made evaluation of multistate models incorporating multiple sources and types of data, such as from telemetry and tag return, more practical for fisheries biologists (Kéry and Schaub 2012). Thus, telemetry analyzed in a multistate framework can be an optimal method to estimate various components of fish mortality. The purpose of this article is to provide an overview of field designs and analytical approaches that can be used to estimate mortality using telemetry. The aspects of field design we evaluate include use of fixed receivers versus manual searches, whether or not to use external tags, and the sample size needed to minimize bias and achieve useful precision. Following Kéry and Schaub (2012), we illustrate the use of multistate capture-recapture models for data analysis. These models provide an intuitive way of describing a fish’s state (e.g., alive, natural mortality) and the state transitions that are possible from one period to the next (e.g., alive to natural mortality). Rapid advances in telemetry technology suggest that these methods will be increasingly useful for future studies of fish mortality.
high-reward tags, as an alternative approach for estimating $F$ and $M$, and (D) manual searches, telemetry with external high-reward tags: to estimate $M$ and fishing mortality rates associated with harvest ($F_h$) and catch and release ($F_c$) as well as the probability of death due to catch and release ($\alpha$).

We evaluated the designs with multistate capture-recapture models, fitted using a state-space likelihood (Kéry and Schaub 2012; Servanty et al. 2014). Multistate models are very useful for ecological studies because they distinguish between true states (“the data we wish we had”: Link and Barker 2010) and what we actually observe. A fish’s true state (e.g., “alive” or “alive without an external tag”) can be estimated if not known; observations depend on study design and the fish’s state. For example, in a study using only manual searches, a fish in the alive or “natural death” state can either be detected or not detected, but a “harvest” fish can only be not detected (because that design assumes that harvested fish lack an external tag). A fish that is not detected at time $t$ might be dead (i.e., harvest or natural death) or alive, with a probability that depends on the entire sequence of observations up to time $t$. For example, if 1 is a live detection and 2 is not detected, then a fish with capture history 12221 is in the alive state at time 3 even though not detected in that interval, whereas the state of a fish with capture history 12222 is unknown at time 3. The estimate for the state of this fish in time 3 would depend on the magnitude of detection probability; the higher the detection probability, the more likely this fish’s estimated state would be harvest. Observations for all telemetered individuals are summarized as a “capture history” matrix, with rows for telemetered individuals and columns for periods.

Models include statements describing the transition probabilities from one state to another. For example, survival rate is the probability of a fish remaining in the alive state from one period to the next, whereas exploitation rate is the probability of transitioning from alive to harvest. The states that a fish can transition into depend on its current state; for example, in a study with fixed receivers only, a fish can remain in the alive state (with probability $S$ for survival) or transition into the dead state with probability $1 - S$. Transition probabilities at each time step sum to 1.

Telemetry estimates of mortality can be daily, monthly, seasonal, or annual depending on the study design. Here we assume studies were conducted over five periods (i.e., tracking at the start of periods 2–5 to estimate mortality for intervals 1–2, 2–3, …), as might occur with quarterly monitoring. We assumed that an equal number of tagged fish entered the study at the start of periods 1–4, in order to maintain an adequate sample size throughout the study. Fish used in analysis were assumed to have cleared a “probationary” period, to eliminate potential capture and tagging classification could be made based on habitat; for example, a detected–natural mortality. However, any movement of dead fish must be confirmed states, (2) the probability of transmitter failure or expulsion ($\beta$); dead fish have a 0 probability of being observed. The detection pattern for an alive fish will depend on receiver spacing and movement rates for that species. In practice, when a fish is detected, it is assumed to be alive, but it is important to examine the temporal and spatial patterns of detections to exclude a dead fish (carcass) that is detected because it is in range of a receiver (or set of receivers). For this design, continuous detections of a dead fish should be scored as not detected in the capture history.

Scoring a fish as detected in the capture history (indicating an alive state) could be based on movement such as detections on more than one receiver or two sets of detections on a single receiver, with sufficient time in between to establish that the fish moved away then returned within range (Harris and Hightower 2011); however, it may be important to account for any potential movement of dead fish, as might occur if the carcass floats downstream or if the individual is consumed by a moving predator or scavenger (Muhametsafina et al. 2014). Although not considered here, spatially explicit capture-recapture models can also be used to estimate survival probabilities from the pattern and number of detections at a grid or linear array of fixed receivers (Gardner et al. 2010; Raabe et al. 2014).

**Manual Searches, Telemetry Only**

Our second design assumes that a manual search of the study area is done each period. Searching provides a substantial improvement over passive detections at fixed receivers, because total mortality can now be partitioned into fishing and natural rates by examining the pattern of detections in both time and space (Hightower et al. 2001). The multistate model for this design has three possible states: alive, natural death, and harvest (Figure 1b). Live fish can remain in the alive state or transition to either of the other two states. Observations for each period are of three types: detected–alive (state = alive), detected–natural death (state = natural death), and not detected (all three states possible). Thus, each simulated capture history matrix has one row for each telemetered fish, with a 1 for detected–alive, 2 for detected–natural death, and 3 for not detected.

In general, a change in location from one period to the next (above purely random error in estimating position) would provide a detected–alive observation and a transmitter that remained in the same location over time would be classified as a detected–natural mortality. However, any movement of dead fish must be accounted for and periods of quiescence should not be mistakenly classified as natural mortalities (Stich et al. 2015). In addition, classification could be made based on habitat, for example, a detected–natural death observation could be made by locating a fish in an unsuitable habitat, such as cold or anoxic bottom water or shallow waters occupied by predators (Lee and Bergersen 1996; Bettoli and Osborne 1998; Jepsen et al. 1998). A fish not detected has an unknown state, but the probability of state = harvest would increase rapidly when not detected for multiple periods. The model assumes no catch and release mortality (which would be harvested) were assumed to occur instantaneously at the start of the period of detection.

**Fixed Receivers, Telemetry Only**

This design assumes an array of fixed receivers that telemetered fish encounter through movement. Examples include a lake with PIT antennas (Hewitt et al. 2010) and open systems where receivers are encountered by migrating fish (Lindley et al. 2008; McMichael et al. 2010; Hightower et al. 2015). The multistate model has two possible states: alive and dead (Figure 1a). For this design, observations are only of alive fish (detected with probability $p$); dead fish have a 0 probability of being observed. The detection pattern for an alive fish will depend on receiver spacing and movement rates for that species. In practice, when a fish is detected, it is assumed to be alive, but it is important to examine the temporal and spatial patterns of detections to exclude a dead fish (carcass) that is detected because it is in range of a receiver (or set of receivers). For this design, continuous detections of a dead fish should be scored as not detected in the capture history.

Scoring a fish as detected in the capture history (indicating an alive state) could be based on movement such as detections on more than one receiver or two sets of detections on a single receiver, with sufficient time in between to establish that the fish moved away then returned within range (Harris and Hightower 2011); however, it may be important to account for any potential movement of dead fish, as might occur if the carcass floats downstream or if the individual is consumed by a moving predator or scavenger (Muhametsafina et al. 2014). Although not considered here, spatially explicit capture-recapture models can also be used to estimate survival probabilities from the pattern and number of detections at a grid or linear array of fixed receivers (Gardner et al. 2010; Raabe et al. 2014).
The capture history matrix are 1 for detected–alive, 2 for detected–harvest, subsequent catch-and-release events would not be detected for catch-and-release survivors that lack an external tag; therefore nonharvest deaths would represent natural deaths and undetected catch-and-release deaths.

We assumed that fish in the states alive and natural death have the same time-dependent detection probability $p$, although separate probabilities could be used if appropriate. Fixed receivers could provide supplemental information in this study design, but manual searches are still required unless fish are always within range of at least one fixed receiver (e.g., Heupel and Simpfendorfer 2002). For example, a fish could have a detected–alive observation even if missed on the manual search for that period, if it was detected on fixed receivers in a pattern that established survival (although this might require different detection probabilities for alive and natural death).

**Fixed Receivers, Telemetry with External High-Reward Tags**

Our third design does not require manual searches of the study area but instead uses fixed receivers and returns of external high-reward tags to partition $Z$ into $F$ and $M$. The multistate model for this design has the same three possible states as for the second design: alive, natural death, and harvest (Figure 1b). Codes for the capture history matrix are 1 for detected–alive, 2 for detected–harvest, and 3 for not detected. Live fish can remain in the alive state or transition to either of the other two states. Observations are of three types: detected–alive (state = alive), detected–harvest (state = harvest), and not detected (possible states are alive and natural death). As in design B, we assume no catch and release fishing. We assume that harvest of fish with high-reward tags is reported with probability 1. We also assume no external tag loss.

**Manual Searches, Telemetry with External High-Reward Tags**

Tagging with both a transmitter and a high-reward external tag makes it possible to distinguish true natural mortality from catch and release mortality (Kerns et al. 2012, 2016). Assessment of fishing mortality due to catch and release is especially important when rates of catch and release are high (Kerns et al. 2012). Recreational anglers will often call immediately after catching a fish with a high-reward tag, resulting in very precise information about the timing and location of catch and release events. In this study design, catch and release mortality is assessed by evaluating movement patterns after release and sufficient manual searches need to be completed to establish whether a fish survived catch and release or not. Estimates of catch and release mortality based on fish movements should be superior to estimates from cage studies, because of biases due to confinement and the difficulty of obtaining true control fish (Pollock and Pine 2007). The time frame for manual tracking to detect a catch and release death might differ by species and environmental conditions but we assume a relatively short interval (e.g., less than one week) in order for true natural mortality to be assumed negligible. The appropriateness of this assumption depends on the interval length and the magnitude of natural mortality for fish not caught during the period. Telemetry also allows for the evaluation of any sublethal behavioral effects of catch and release (Donaldson et al. 2008; Lennox et al. 2015).

The multistate model in this case is much more complex, with eight possible states: (1) alive with external tag, (2) catch and release survivor, (3) alive without external tag, (4) natural death, (5) nonharvest death, (6) catch and release death, (7) harvest with external tag, and (8) harvest without external tag (Figure 1c). Fish that are alive with external tag can remain in that state or transition into states natural death, harvest with external tag, or the two catch and release states. A fish in the catch and release survivor state can transition into state 3 by surviving, be removed from the system by harvest without external tag (i.e., transition to state 8), or transition into state 5, which combines natural deaths and deaths due to undetected catch and release (i.e., because the fish lacks an external tag to indicate catch and release). Fish that transition into state 3 similarly can remain in that state (survival, including undetected catch and release events), transition into state 5, or be harvested.

Observations are of eight types and are made by manual searches and returns of high-reward tags. The entire study area is searched on each occasion. A transmitter detected in the same location for multiple periods would be scored as a detected–natural death (state 4) if the fish had an external tag, a nonharvest death (state 5) if its external tag had previously been clipped, or a catch and release death (state 6) if occurring immediately after a reported catch and release. A change in location from one period to the next would establish that the fish was alive (i.e., in state 1 or 3, depending on the status of the external tag). Whether alive or dead, fish remaining in the study area are either detected with probability $p$ or not detected with probability $1 − p$. We assume that external tags are clipped and returned for all fish that are harvested or caught and released; thus, harvest and catch and release events for a fish with a high-reward tag would be known with
probability 1. The probability of dying due to catch and release is represented by parameter $\alpha$, which is estimated by the model. Although not illustrated here, reported high-reward tags of harvested fish could also be used to partition fishing mortality among sectors, such as commercial versus recreational. For a fish with a cut high-reward tag, harvest would only be detected indirectly based on not being detected for multiple periods. Additional assumptions for this model are no external tag loss or nonreporting, and that all transmitter removals are harvest.

**Analysis**

Estimates were obtained for four period-specific mortality rates (defining the probability of survival from time 1 to time 2, etc.) and detection probabilities. For the first three designs, the simulated data were generated using $F_s$ of 0.2, 0.1, 0.3, and 0.2 and $M$s of 0.10, 0.15, 0.15, and 0.10. We estimated $Z$ rather than $S$, the survival rate, for design 1 (i.e., fixed receiver, telemetry only) for consistency with the other three designs. For the fourth design, which also accounted for catch and release, $M$ was unchanged and we kept $Z$ the same as in the other three designs by reducing $F_s$ ($F_s' = 0.16, 0.08, 0.24, 0.15$) to allow for mortality due to catch and release ($F_r = 0.04, 0.02, 0.06, 0.05$). The probability of dying due to catch and release ($\alpha$) in our simulations for design D was 0.1. Following Jiang et al. (2007), we estimated $\alpha$ and $F_r$, the rate of mortality for tags of caught-and-released fish. The mortality rate for fish caught and released is $F_r = \alpha F_s'$. Our simulations assumed that detection probability was 1.0 at the start of the study (all fish alive and detected) but varied arbitrarily for periods 2–5 (0.8, 0.8, 0.6, 0.9). Detections provide information about survival up to that point; for example, a detected–alive observation at period 3 establishes that fish’s survival from release to time 3, even if not detected in period 2. Time-dependent detection probabilities might occur due to uncontrollable factors such as weather, boat noise, and fish distribution. Detection probabilities were estimated as time-dependent, fixed effects. For studies with a greater number of periods (typically 10 or more; Burnham and White 2002; Kéry and Schaub 2012), detection probabilities can be modeled as random effects (Kéry and Schaub 2012). Estimating detection probabilities as random effects means that they are not independent but are drawn from a common distribution. This can increase precision and avoid the confounding that can occur between the last survival estimate and the last detection probability, if both are estimated as fixed effects (Kéry and Schaub 2012). To avoid confounding between our final estimates of mortality and detection probability in our simulations, we included a second likelihood component for an independent follow-up search, using fish detected in the final period as the sample size for a binomial experiment with a closed population. To illustrate, assume that 10 fish were detected on the final search and that the true (unknown) detection probability was 0.5. If a follow-up search was done using the same search protocol, the expected result would be to detect 5 of those 10.

Parameter estimates for all models were obtained using R and JAGS (Plummer 2003; R Core Team 2014). R is a general statistical software package that we used to generate simulated data to test parameter estimation under each field design. Parameter estimates using the simulated data were obtained using JAGS, a Bayesian statistical software package. The code we used was modified from Kéry and Schaub (2012). Telemetry analyses can also be done using frequentist methods, but we agree with others (Kéry 2010; Kéry and Schaub 2012; Dorzaio 2016) that the BUGS language (Lunn et al. 2000; JAGS and other variants) promotes clarity of thinking about the problem and the analysis. It is also straightforward to tailor Bayesian analysis code to fit a specific field design; for example, our additional simulated search after the study’s end or a study combining tag-return and telemetry components. Bayesian methods are particularly useful when sample sizes are small (as is often the case with telemetry) or when using hierarchical models that relate observations to latent state variables of interest (Dorazio 2016). A Bayesian analysis takes into account both prior knowledge and new data to produce an estimate of the posterior distribution (McCarthy 2007). We assumed no prior information and used prior distributions for model parameters that were intended to be uninformative. We used a uniform (0, 2) distribution for mortality parameters (because instantaneous rates sometimes exceed 1) and a uniform (0, 1) prior distribution for $\alpha$ and the detection probabilities.

We evaluated the performance of each study design using a sample size of 25 to 100 telemetered individuals entering the study at the start of periods 1–4 (Appendices A–E, Supplemental Material). It seems unlikely to get reliable estimates with an initial sample size of less than 25; 100 should be more than adequate for estimation but costly. We used an automated function (autojags) that updated estimates in increments of 2,000 until our convergence criterion was met for all parameters (Brooks-Gelman-Rubin diagnostic $R < 1.1$; Gelman and Shirley 2011). We discarded the first 1,000 estimates as a burn-in and used three independent chains for updating parameter estimates. Convergence was rapid and produced a sample size of at least 3,000 for posterior distributions. We did not test for goodness-of-fit of our simulated data but that is an important step in analysis of field data. Kéry and Schaub (2012) demonstrate a technique (posterior predictive checking) that is straightforward in a Bayesian analysis.

We used percentage relative error ($PRE = 100 \times \frac{[\text{estimate} - \text{true}]}{\text{true}}$; Vandergroot and Brendan 2015) to assess bias in model estimates and the coefficient of variation (CV = SD/estimate * 100) to assess precision. Our sample size recommendations were based on a target CV of 25%, which in the absence of bias should result in estimates within ±50% of the true values. Robson and Regier (1964) suggested that ±50% represented a useful level of accuracy for management surveys or preliminary studies. Our plots relating sample size to CV can be used to evaluate the cost of achieving other target levels of precision.

**RESULTS**

Estimates in our simulated studies generally appeared to be unbiased, although we observed positive bias (median PRE greater than 0) for the latter three designs when the number of telemetered fish was low (Figure 2). Precision was generally similar among designs, increased with sample size, and was greater for $Z$ than the component rates (Figure 3). Precision generally increased in periods 1–3 as the number of telemetered fish at large increased but then decreased in period 4 because of uncertainty in the final period about the fate of undetected fish. Estimated CVs for $Z$ were mostly less than the target of 25% but that level of precision was not often achieved for component rates. Precision for $Z$ estimates was lower for design A than for designs B–D. Estimates of component rates were more precise when that source of mortality was directly observed (i.e., $M$ in design B, $F_r$ in design C). Lower precision was estimated for $F_r$ in design D compared to the other component rates, likely because mortality due to catch and release fishing was assumed to occur infrequently (0.1 probability).
DISCUSSION

Our simulations show that telemetry can be an effective means of estimating total mortality and its component rates using Bayesian methods and multistate models. The results should be helpful in designing a study with minimal bias and acceptable precision (i.e., choosing a field design, sample size, and pattern of releases). Recent examples using telemetry alone or in combination with conventional tags have shown its potential for transforming fishery management; for example, showing that assumed natural mortality rates were too high (Striped Bass *Morone saxatilis*: Hightower et al. 2001; Red Drum *Sciaenops ocellatus*: Bachelor et al. 2009) or too low (Spotted Seatrout *Cynoscion nebulosus*: Ellis 2014; Striped Bass: Harris and Hightower, in press). These telemetry studies clarify the potential for management through harvest regulation; for example, harvest restrictions may have little benefit for stocks with high environmentally driven natural mortality. Telemetry studies can also quantify seasonal patterns in fishing and natural mortality (e.g., Waters et al. 2005; Thompson et al. 2007; Ellis 2014). Information on seasonality of natural mortality can suggest key mortality sources such as spawning (Waters et al. 2005) or extreme temperature (Ellis 2014), which help us better understand biology, elucidate annual variability in population size, and inform the timing of harvest regulations. Sources of mortality can be evaluated at a very fine temporal scale using telemetry. For example, Ellis (2014) used daily telemetry results to establish a strong connection between extreme cold events and natural mortality of Spotted Seatrout. Conventional tag-return studies can also provide information about seasonality in fishing and natural mortality, especially if tagging is done on a continuous basis to maintain a sufficient number of tagged fish at risk (e.g., Ellis 2014). Potential advantages of a combined tagging–telemetry approach are that direct information on various sources of mortality may be possible (e.g., external tags can directly inform on harvest from multiple fisheries including catch and release and tournament fishing [Kerns et al. 2016] and manual searching can directly inform on multiple types of natural death).
and that sample size can be increased, leading to higher precision and reduced bias (Pollock et al. 2004; Kendall et al. 2006).

The four designs considered here range widely in the amount of effort required (beyond the substantial effort for capture and tagging). The first design simply requires that a receiver array be maintained, and estimates of total mortality can often be obtained as an effortless byproduct of ecological studies. For example, Lindley et al. (2008) used fixed receiver detections to estimate apparent annual survival of telemetered Green Sturgeon *Acipenser medirostris* that encountered fixed receivers during migrations along the U.S. Pacific Coast. The survival estimate was assumed to be a minimum rate because it would be negatively biased by any transmitter failures or expulsions, tagging mortality, or emigration from the study area. Estimates of \( Z \) from design A in our simulated studies were unbiased although precision was typically lower than for the more labor-intensive or costly designs B through D. Our designs B and C allow for partitioning \( Z \) into \( F \) and \( M \) and estimates were generally similar in terms of bias and precision, although we did observe higher precision for the parameter based on direct observation (\( M \) for design B, \( F \) for design C). Choosing between the two designs could depend on which parameter (\( M \) versus \( F \)) was of greater management concern or biological interest but may also depend on logistical considerations. The second design requires manual searches so it is only practical in smaller systems, but it does not rely on external tags or the assumption of 100% reporting. In contrast, the third design using high-reward tags could be done in large or even open systems (assuming no permanent emigration) but it relies on 100% reporting. The fourth design is the most demanding, in that it requires high-reward tag returns and manual searching, but it addresses catch and release fishing, which is increasingly important in many systems. An alternative (and simpler) form of design D would be to use the absence of live detections to indicate natural mortality (as in design C), although manual searches would still be required to assess catch and release mortality.

Our estimates were generally unbiased except when compu-
nent rates were estimated and sample sizes were small (e.g., releases of 25 fish per occasion in period 1). The cause of bias is unknown but is likely due to the effect of the prior distribution, given the absence of bias in later periods and for larger sample sizes. Improved estimates in future field studies might be obtained by releasing a greater proportion of the total sample size at the start of the study (with remaining fish in staggered releases to maintain a sufficient sample size). The merits of a particular release pattern will depend on mortality rates (whether the pool of telemetered fish builds up or declines between searches).

Estimates obtained using Bayesian methods take into account both the prior information and new data. When no prior information is available (as is often the case and as assumed here), having to specify a prior distribution is sometimes viewed as a disadvantage of Bayesian methods (Dorazio 2016). In addition, when sample sizes are small (again, as is often the case for ecological studies), the choice of a prior distribution can have an effect on model estimates. Instantaneous mortality rates are challenging to estimate because they are nonnegative but can be close to 0 (especially for short study intervals), unbounded on the upper end, and used both in arithmetic scale and exponentiated (e.g., \( \exp(-F-\alpha) \)). Prior distributions that are uninformative on one scale are likely to be informative on another (Punt and Hilborn 1997; Meyer and Millar 1999; Maunder 2003; Dorazio 2016). Bayesian stock assessment models typically use a uniform (Hilborn and Mangel 1997) or lognormal prior distribution (McAllister and Ianelli 1997; Millar and Meyer 2000) for mortality rates. In the absence of true prior information, Punt and Hilborn (1997) suggested the use of an uninformative prior by testing alternatives to evaluate sensitivity. We encourage potential users of these methods to examine bias and precision using simulation with mortality and detection probabilities, sample sizes, and patterns of releases relevant for the planned study.

The assumptions required for these methods are generally similar to other tagging studies, but there are some practical issues that are unique to telemetry studies. For example, detection probabilities could vary between live fish and natural deaths (designs B and D) if transmitters from natural deaths were more difficult to detect over time because they became embedded in the substrate. This could be evaluated experimentally; for example, by releasing euthanized fish with transmitters and checking regularly for those tags (Muhametsafina et al. 2014). Transmitter failure appears to be rare (although see Kerns et al. 2016) but can be monitored by setting aside tags or regularly detecting transmitters of known mortalities (e.g., Hightower et al. 2001). Transmitter expulsion is difficult to assess other than through tank or pond studies (e.g., Friedl et al. 2013). Detecting and censoring fish that emigrate is a key element of designs B and D, because manual searches of the study area are done to differentiate between natural deaths and harvest. Designs A and C do not require manual searches but assume that there is no permanent emigration. Performance of receiver gates to detect emigration can be assessed using multiple tows of a test tag (Melynchuk 2012), but it is difficult to cover all environmental conditions. Having multiple gates at exit points is ideal in that it not only allows estimation of detection probabilities by gate (e.g., Melynchuk 2012) but also reduces the probability of exiting undetected.

Careful examination is required to ensure that raw detections are classified without error. For example, detections in different locations are generally interpreted as a live detection observation but could be movement of a predator that had consumed a tag (Muhametsafina et al. 2014). Movement parameters such as swimming speed or tortuosity of the migration route can sometimes be used to infer that a transmitter was consumed by a predator or scavenger (Bacheler et al. 2009; Friedl et al. 2013; Romine et al. 2014; Gibson et al. 2015). Predation events can also sometimes be confirmed by sampling; for example, Jepsen et al. (1998) documented salmon smolt predation by collecting predators that contained transmitters. Our models assume no errors in state assignments, but it is possible to develop multistate models that allow for state misclassification. Stich et al. (2015) developed a state-space multistate model similar to those in this article to analyze telemetry data for Grass Carp Ctenopharyngodon idella, a highly sedentary fish that could be alive but mischaracterized as dead by lack of tag movement or an erroneous signal from a mortality-sensing tag. Consideration of the biology of the species is important in study design and assessment of observations; however, in most situations, a manual review of detections is straightforward, can be done using a set of rules to promote objectivity, and provides other useful ecological data such as movement patterns.

In summary, we have shown that state-space multistate models can generate useful estimates of fish mortality rates from telemetry data. They also clarify the connection between field observations and the latent states that are of interest. Extended versions of these models could account for practical issues such as tag loss, temporary emigration, or nonreporting. The ability to generate accurate information on survival, along with movement and behavior information, could make telemetry an important component of a sampling program for stock assessment and fisheries management purposes, although sampling design, sample size, and assumptions should be considered carefully in relation to the biology of the species, the sources of mortality for the population, and the questions to be addressed. The R and JAGS code included as supplementary material can be used to explore the potential of a proposed telemetry study to provide reliable mortality estimates by changing population rates (e.g., \( F, M, \alpha \)), number of periods, sample size, etc. The flexibility of JAGS software means that relatively minor code alterations could be made to answer a suite of questions on multiple components of mortality, as needed for management and conservation.

ACKNOWLEDGMENTS

We thank three anonymous reviewers for comments on a previous draft.

SUPPLEMENTARY MATERIALS

Supplemental material for this article can be accessed on the publisher’s website at 10.1080/03632415.2017.1276347.

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