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Tagging Methods for Estimating Population Size and Mortality Rates of Inland Striped Bass Populations

Joseph E. Hightower*
U.S. Geological Survey
North Carolina Cooperative Fish and Wildlife Research Unit
Department of Biology, North Carolina State University
Raleigh, North Carolina 27695, USA

Kenneth H. Pollock
Departments of Biology, Biomathematics, and Statistics
North Carolina State University
Raleigh, North Carolina 27695, USA

Abstract.—Striped bass *Morone saxatilis* in inland reservoirs play an important role ecologically and in supporting recreational fishing. To manage these populations, biologists need information about abundance and mortality. Abundance estimates can be used to assess the effectiveness of stocking programs that maintain most reservoir striped bass populations. Mortality estimates can indicate the relative impact of fishing versus natural mortality and the need for harvest regulation. The purpose of this chapter is to evaluate tagging studies as a way of obtaining information about abundance and mortality. These approaches can be grouped into three broad categories: tag recapture, tag return, and telemetry. Tag-recapture methods are typically used to estimate population size and other demographic parameters but are often difficult to apply in large systems. A fishing tournament can be an effective way of generating tagging or recapture effort in large systems, compared to using research sampling only. Tag-return methods that rely on angler harvest and catch and release can be used to estimate fishing (*F*) and natural (*M*) mortality rates and are a practical approach in large reservoirs. The key to success in tag-return studies is to build in auxiliary studies to estimate short-term tagging mortality, short- and long-term tag loss, reporting rate, and mortality associated with catch and release. *F* and *M* can also be estimated using telemetry tags. Advantages of this approach are that angler nonreporting does not bias estimates and fish with transmitters provide useful ecological data. Cost can be a disadvantage of telemetry studies; thus, combining telemetry tags with conventional tag returns in an integrated analysis is often the optimal approach. In summary, tagging methods can be a powerful tool for assessing the effectiveness of inland striped bass stocking programs and the relative impact of fishing versus natural mortality.

* Corresponding author: jhightower@ncsu.edu

Introduction

Striped bass *Morone saxatilis* have been widely introduced into inland reservoirs, not only to provide recreational fishing opportunities, but also to fill an ecological role as a top-level predator. These introductions have generally been successful, but most populations are maintained by stocking because, with few exceptions, striped bass do not reproduce in reservoirs. Management of these stocked populations is generally limited to combinations of size and creel limits to control harvest. Information regarding population size or mortality rates would be helpful in developing or assessing regulations and stocking rates, but striped bass populations are difficult to survey because of their pelagic distribution (Moore et al. 1991).

Prior studies have shown that a variety of data sources can be combined to estimate approximate population size of striped bass in large reservoirs. For example, Moore et al. (1991) used age-composition data from standardized gill netting to generate a catch curve (Ricker 1975) estimate of the total mortality rate for striped bass in Smith Mountain Lake, Virginia. Natural mortality was thought to be low, so the exploitation rate was assumed to be equal to the total mortality rate. They then obtained an estimate of age-4 abundance by dividing a creel survey estimate of 1977 age-4 harvest by the assumed exploitation rate. That abundance estimate was used to scale up gill-net catch-per-unit-effort data in order to estimate abundance for other ages and years. Cyterski et al. (2002) produced additional estimates of abundance for Smith Mountain Lake striped bass. They used the average number of stocked juveniles and survival estimates from gill-net data to generate a population vector. For the reproducing striped bass population in the Santee–Cooper system in South Carolina, Bulak et al. (1995) estimated population size from estimates of egg production in tributary rivers, a mark–recapture estimate of juvenile abundance, a published estimate of juvenile mortality, and catch-curve estimates of mortality for fish age 1 and older.

A large-scale tagging study can provide direct estimates of population size and mortality that would be useful for management. For example, tagging estimates of population size can be used to evaluate stocking success or to adjust stocking rates. Population estimates can also be used in bioenergetic models to examine the balance between predators and prey resources (Cyterski et al. 2002). Fishing and natural mortality estimates from a tagging study can be used to construct yield models in order to examine the potential benefits of different fishing mortality rates or size limits (Thompson et al. 2007). Information about fishing versus natural mortality is also helpful in determining whether a stocking program is meeting its goal or whether other factors (e.g., poor habitat quality) limit the program's potential (Hightower et al. 2001).

The purpose of this chapter is to examine various tagging methods (tag recapture, tag return, telemetry) to determine what types of estimates each method can provide and then suggest under what conditions the method would be practical in the field. We also include guidance about the reliability of tag-return estimates as a function of study design and mortality rates. This review of tagging methods is directed towards striped bass researchers but should be equally relevant for fisheries biologists studying hybrid striped bass and other fish species in large reservoirs.

Tag-Recapture Models

Closed tag-recapture models are used to estimate population size. The simplest version is the Petersen model for two sampling occasions (Ricker 1975; Seber 1982). It is applicable in short-term studies where the population is closed (no changes due to recruitment, mortality, emigration, or immigration). We provide below an overview of the Peterson model and then consider more general models for three or more sampling occasions. There are versions of these more general models for situations where the animals may have unequal capture probabilities due to heterogeneity (variation among individuals) or trap response (where being captured affects the odds of being caught again). Open models allowing for recruitment, mortality, emigration, and immigration are used to estimate population sizes and other demographic parameters.

Petersen two-sample model

The Petersen closed population model has a long history and can be applied whether tagging and recapture are done solely by the researcher or whether angler catches provide fish for tagging or recapture. This approach assumes that the population is closed (no mortality and no recruitment or migration in or out), so sampling would need to occur over a month or two, given the typical annual survival rate of 40% for adult striped bass (e.g., Moore et al. 1991; Bulak et al. 1995; Hightower et al. 2001; Young and Isely 2004; Thompson et al. 2007).

For inland striped bass, a two-sample population estimate could be obtained by research gill netting. A practical concern about relying on research collections for tagging and recapture is that for a large and widely dispersed reservoir population, it is difficult to achieve a suitable capture probability (probability of capturing an individual on a sampling occasion). For a reservoir population estimate, capture probability can also be thought of as the fraction of the population sampled on each occasion. As an example, consider a 4,000-ha reservoir that could have 65,200 age-1 and older striped bass (based on the estimate of 16.3/ha from Moore et al. 1991). Guidelines from Robson and Regier (1964) suggest that a two-sample Petersen estimate should be based on capture of roughly 2,000 fish in each of the two samples in order to be within 25% of the true population size (i.e., between 48,900 and 81,500). Capturing 2,000 fish on each occasion from a population of 65,200 is a capture probability of about 0.03, which is low but would still be difficult to achieve in practice. The highest average gill-net catch per unit effort for Smith Mountain Lake was 10.06 (age 1) striped bass per overnight set of three gill nets (Wilson 2004), which implies that 200 three-net sets would be needed to achieve a sample size of 2,000 fish. Another practical issue is that mortality associated with gill-net capture would need to be measured and accounted for in the population estimate.

An alternate approach would be to take advantage of the sampling effort generated by recreational anglers. For example, Baldwin et al. (2003) estimated the size of a walleye *Sander vitreus* (formerly *Stizostedion vitreum*) population by tagging fish caught in a fishing tournament and obtaining recaptures through short-term gill netting and electrofishing. This approach of using different gears for tagging and recapture was recommended by Ricker (1975), since it would be unlikely for the same biases to be present in both gears. One concern about using tournament catches for the tagging sample is the potential for hooking (tagging) mortality in striped bass. Edwards et al. (2004) tagged largemouth bass *Micropterus salmoides* by electrofishing and obtained recaptures through fishing tournaments on two Connecticut lakes. If a fishing tournament is used to obtain recaptures for a two-sample Petersen estimate, the second sample should be the entire catch of the tournament, with all the fish examined for tags. If fish released during the day ("culled") provide tag returns, it would also be necessary to include the number of culled fish in the second sample. Tag returns from anglers (nontournament fishing) could be used as the recaptures, but this approach is subject to much greater uncertainty compared to a tournament because the size of the second sample (total harvest) would need to be estimated through a creel survey. Nonreporting of tags is a potentially large bias in using fishery tag returns as recaptures. We postpone further discussion of reporting rate to when we discuss tag-return models to estimate fishing and natural mortality.

General tag-recapture models

Tag recapture typically refers to the situation where capture, tagging, release, and one or more live recaptures are made by the researcher. This is distinctly different from tag-return studies (discussed later) that utilize angler harvested tag returns to obtain one recapture. Tag-recapture models are generally categorized as either closed, with the population totally static during the short study, or open, where allowance is made for changes due to births, deaths, emigration, and immigration.

If the focus is on estimating population size and not mortality rates, a short-term study is recommended so that the population can be assumed to be closed (Pine et al. 2003). The Petersen model for two samples is the simplest closed model and has been discussed in the previous section. More general closed population models for more than two samples have a long history, going back to Schnabel (1938). The Schnabel method is very simple and requires the strong assumption of equal capture probabilities of all fish on each sampling occasion (no heterogeneity and no trap response). This approach can be used on a large lake, although it is difficult in practice to obtain large enough samples for tagging and recapture. Hansen et al. (2008) used multiple occasion sampling and a Schnabel model to generate population estimates of lake trout *Salvelinus namaycush* in a 38,300-ha lake. Large trap nets were used to estimate abundance of mature fish during fall spawning periods in 2 years, and gill nets were used in a third year to generate an estimate applicable to all sizes (not just mature fish). Although the estimates required substantial effort (709–1,039 trap-net-nights in the first 2 years and 137 gill-net-nights in the third season), they provided valuable guidance to fishery managers about the current and future effects of this introduced species on native fauna.

The original Schnabel model has been generalized to allow for heterogeneity and trap response to influence capture probabilities (Otis et al. 1978). Those models are available through the software programs CAPTURE and MARK (Otis et al. 1978; White and Burnham 1999; Pine et al. 2003) and would be very useful in situations where abundance was the parameter of interest. In most cases, however, the primary focus for inland striped bass has been on estimating mortality, so we do not discuss them in detail here.

Open tag-recapture models (allowing births, deaths, emigration, and immigration) are the appropriate choice for longer-term studies. They provide information about abundance and mortality, but they have higher data requirements because there are more parameters to estimate. In addition to population size, there are parameters related to losses (apparent mortality, which is usually confounded with emigration) and gains (apparent recruitment, which is usually confounded with immigration). We have found very few published examples of these models being applied in lakes or reservoirs (Hightower and Gilbert 1984; Fabrizio et al. 1997; Mills et al. 2002; Pollock et al. 2007). For a large population, preliminary estimates of population size and survival (within 50% of the true value) can be obtained from a Jolly–Seber model with six sampling occasions and capture probabilities in the range of 0.02–0.04 (Hightower and Gilbert 1984). For the striped bass example considered above (65,200 fish age 1 and older), this would imply a sample size of 1,304–2,608 fish on each occasion. Such a large sample size would be difficult to achieve, even if sampling could be done at a time when the fish are more aggregated (e.g., during a spring spawning migration).

Tag-Return Models for Mortality Estimation

Tag-return models are commonly used when the focus of the study is on estimating mortality rates rather than population size. These so-called "Brownie models" were originally developed for migratory waterfowl (Brownie et al. 1985); thus, they are an effective approach for large or widely dispersed populations that are harvested, such as inland striped bass in reservoirs. These models are generally used to estimate the total mortality rate, but if information is available about the tag-reporting rate (probability that the tag on a harvested animal is reported), total mortality can be partitioned into harvest and natural death components (Pollock et al. 1991; Hoenig et al. 1998b). These estimates greatly enhance the value of tagging studies as they can be used to determine the need for harvest regulations or to determine if the current harvest rate is at or below a target level.

Tag-return studies are often conducted for a single year in order to get a point estimate of the exploitation rate. The multi-year approach developed by Brownie et al. (1985) produces estimates of annual total mortality, and this can be split into fishing and natural mortality if reporting rate can be estimated. The multi-year approach has higher cost but provides much more information about the demographics of the population. To obtain acceptable results, the study should span at least 3 to 5 years with a release of at least 300 tagged fish per year (Pine et al. 2003). These recommended sample sizes assume no mortality due to capture, handling, or tagging so they should be increased to compensate for any estimated tagging mortality. Tagging is preferably done at a time when fish are aggregated and readily collected for tagging. For example, tagging of the Roanoke River striped bass population occurs each spring when the fish are concentrated on the spawning grounds (Thomas et al. 2008). Tagging of the coastal migratory striped bass stock occurs during winter when the fish are aggregated off the coasts of North Carolina and Virginia (Welsh et al. 2007). In both cases, tag returns occur throughout the year, from recreational and commercial fisheries and from across the entire geographic range of the population. This wide temporal and spatial coverage would not be practical if dependent on research sampling for recaptures.

Assumptions of tag-return studies include (1) that tagged fish are representative of the entire population, (2) that there is homogeneity of the mortality processes over all fish considered in the model, (3) that the fates of tagged fish are independent, and (4) that tag returns are correctly reported by year (or period, if using a time step other than annual). There are quite a few potential fates of tagged fish (Figure 1), and the study should include auxiliary studies to account for potential biases such as tag loss and mortality due to the tagging process. Information about those factors could be taken from the literature, but every study is unique (e.g., skill level for taggers, water temperatures when tagging done) so using published values introduces an unknown bias. It is far preferable to estimate the rate of tag loss by double-tagging a proportion of fish and noting how many recoveries from double-tagged fish include one versus two tags. Mortality associated with tagging and immediate tag shedding can be estimated through short-term cage (holding pen) studies. Holding pen studies must be carefully designed to avoid bias (Pollock and Pine 2007). For example, mortality due to the holding pen can be accounted for by comparing survival of tagged and control fish, with the latter group treated identically except for the tagging process.

A critical step in conducting a tag-return study is to build in a method for estimating the tag reporting rate so that total mortality can be partitioned into fishing and natural mortality components. A common approach for estimating the reporting rate is through the use of high-reward tags (Pollock et al. 2001). The value of each high-reward tag is assumed to be high enough (e.g., $100) to ensure 100% reporting so the reporting rate can be estimated by comparing the tag-return rate for high-reward versus standard tags (Pollock et al. 2001). High-reward tagging should be done every year; otherwise, one must also assume that reporting rate is constant over years. Other approaches for estimating the tag reporting rate are through the use of planted tags (secretly planting tags in fishers' catches) or getting recoveries through an observer or creel sampling program (Hearn et al. 1999, 2003).

Another important step is to ensure that tagged fish are well mixed within the population as a whole (Hoenig et al. 1998a). This can be difficult to achieve if tagging is done on an aggregated subset of the population (e.g., spawners below an upstream dam) because

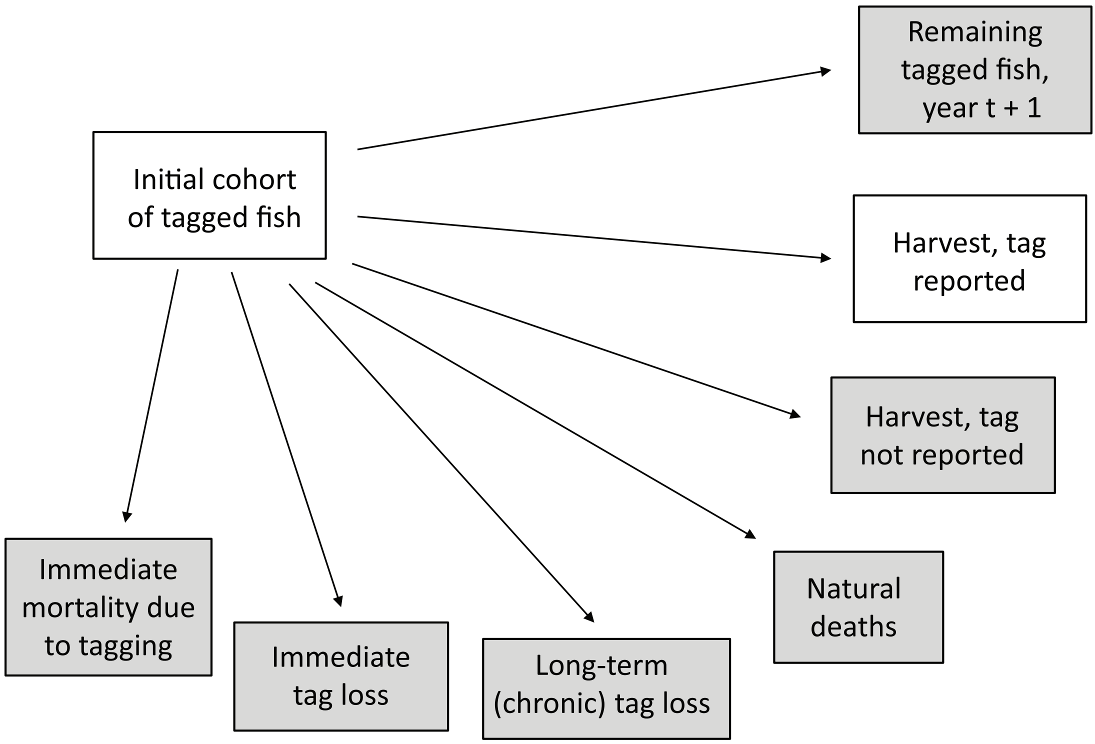

FIGURE 1. Possible fates of tagged fish in a tag-return study. Unfilled boxes are observed (initial number released, reported harvest); boxes with gray shading are fates that are not observed.

those aggregations attract fishing activity. This can result in many tag returns after only a short period at large and may overstate the true intensity of fishing. One analytical approach for dealing with nonmixing is to estimate separate mortality rates for newly tagged and previously tagged fish (Hoenig et al. 1998a). However, this reduces the sample size for the parameters of interest: those that apply to the untagged population. To avoid this consequence, the best approach (if possible) is to spread tagging effort widely across time and space. Information about the spatial distribution of striped bass (such as from telemetry) would be useful for allocating tagging effort.

Another consideration is whether the model needs to account for fish age (size). This might be necessary if vulnerability to harvest (or catch and release) varied substantially by size, for example, due to a minimum size regulation. If only fish above a minimum size limit are tagged, then the standard instantaneous-rates tag-return model for adult fish (Hoenig et al. 1998a) should suffice. If some tagged fish are below the minimum harvestable size, the most practical approach is to use an age-structured model (Jiang et al. 2007) and set up the age-specific vulnerabilities to account for size effects.

The tag-return model must also account for tag returns from catch and release as well as harvest. If the tag is clipped when a fish is caught and released, it reduces the pool of tagged fish at risk but does not contribute to fishing mortality (except for catch-and-release mortality, discussed below). This can be accounted for analytically by modeling the population of tags at risk, rather than tagged fish (Jiang et al. 2007). An additional fishing mortality rate F' is introduced to account for the "mortality" of clipped tags. The population of tags declines due to fishing (F), clipping of tags for fish caught and released (F'), and natural mortality (M), so the total instantaneous mortality rate (Z) for tags is $F + F' + M$. Z for fish is $F + \delta F' + M$, where δ is a value between 0 and 1, accounting for mortality due to catch and release. The probability of catch-and-release mortality has to be estimated from some kind of auxiliary study (Bettinger and Wilde 2013, this volume). Reported tags from fish that are caught and released with the tag left intact are difficult to account for analytically. The situation is somewhat similar to the tag-recapture models discussed earlier, but in this case, recaptures by anglers occur at random times (rather than on a set schedule of research sampling occasions). More work is needed on this topic because very valuable information could be gained if fish were recaptured (caught and released) multiple times. Until new modeling approaches can accommodate these data, two practical options are to ignore those reported tags (Jiang et al. 2007) or to treat those tags as if they had been clipped (ignoring any later reports of those tags; Bacheler et al. 2008).

The precision of tag-return estimates depends on the number of returned tags, which depends on the number of tagged fish, rates of fishing and natural mortality, the reporting rate, and the number of years of recoveries. A biologist planning a tag-return study can use simulation with assumed rates to determine how many fish to tag in order to obtain useful results. Appendix 1 contains simulation code for program SURVIV, which can be run using a Web browser (www.mbr-pwrc.usgs.gov/software/survive.html).

The example is based on a standard Brownie model with 3 years of releases (at 200 fish per year) and 5 years of tag returns. The relative standard errors (SE/estimate × 100) show that precision is excellent for the survival rate (assumed constant over the experiment) and tag-return rates for years 1–3 (Table 1). The precision of survival estimates would be substantially reduced if estimated separately for each year. Precision of recovery rate estimates decreases considerably for the final 2 years, when no additional tags are released. The example code can be modified to explore how changes in study design or the assumed rates affect the expected precision (e.g., change number of released tags to 100 per year).

Tag-return methods are designed to estimate mortality rates, but it would be possible to estimate population size as well if a creel survey estimate of harvest was available. The tag-return estimates of F and M would be used to calculate an exploitation rate: $u = F/Z \cdot [1 - \exp(-Z)]$. Dividing the creel survey estimate of harvest by the exploitation rate would provide an estimate of abundance for fish within the exploited size range. There would be considerable uncertainty associated with an estimate of this type because it would include variance components due to the tag-return estimates of F and M and due to the creel survey estimate of harvest. Before planning a field study that would use this approach, it would be wise to simulate the tagging experiment (as in Appendix A) and to obtain at least a rough estimate of the variance for the creel survey estimate of harvest. An approximate variance for the population estimate can be obtained using the delta method (similar to equation (12.2) in Williams et al. 2002).

Telemetry-Based Approaches for Estimating Mortality Rates

Telemetry-based methods have proven effective for short- and long-term studies to estimate mortality rates. They differ from the previously described tag-recapture and tag-return studies in that fish with transmitters are rarely captured again after tagging. Instead information comes from "virtual" recaptures, when the telemetered fish is detected and some indication of its status is determined (e.g., its current position or change in position since the last detection).

Short-term telemetry studies have addressed management issues such as catch-and-release (hooking) mortality (Bendock and Alexandersdottir 1993; Lee and Bergersen 1996; Bettoli and Osborne 1998) or mortality associated with downstream passage through turbines (Skalski et al. 2002). These studies typically rely on transmitters that are attached

TABLE 1. Estimated rates, SEs, and relative SEs (SE/estimate × 100) from a simulated tag-return experiment (Appendix 1) with 3 years of releases (200 tagged fish per year) and 5 years of returns, using 100 replicates. Survival was 0.4 for all 5 years and was estimated as a single parameter; true annual recovery rates were 0.4, 0.5, 0.4, 0.5, and 0.4 for years 1–5.

Parameter	Mean estimate	Mean SE	Relative SE (%)
Survival rate	0.404	0.030	7.47
Recovery rate, year 1	0.396	0.032	8.19
Recovery rate, year 2	0.499	0.031	6.25
Recovery rate, year 3	0.399	0.030	7.40
Recovery rate, year 4	0.499	0.073	14.67
Recovery rate, year 5	0.397	0.109	27.39

quickly, either externally or by insertion into the stomach. This can be a better approach for studying catch-and-release mortality of striped bass than cage studies because of the potential for stress or mortality when held in cages (Haeseker et al. 1996; Bettoli and Osborne 1998). On the other hand, the concern for short-term telemetry studies is stress or possible mortality associated with the transmitter. Bettoli and Osborne (1998) noted that their short-term mortality estimates were low except during summer, which argued for a seasonal effect related to catch and release rather than due to transmitter attachment.

Improvements in transmitter and receiver technology have dramatically increased our capability to conduct longer-term studies that are the focus of this article. These studies can provide monthly, quarterly, seasonal, or annual estimates of fishing and natural mortality. The methods and models were first developed for terrestrial populations (Trent and Rongstad 1974; Pollock et al. 1989a, 1989b; White and Garrott 1990; Pollock et al. 1995), then modified for fish because the status of a telemetered fish is generally determined indirectly, through movement (Hightower et al. 2001). The approach requires that the entire study area be searched on a regular basis (e.g., monthly). Telemetered fish that change locations between search occasions are assumed to be alive, those that remain stationary are eventually classified as a natural mortality (or catch-and-release mortality), and those that disappear are classified as harvested. If fish can emigrate from the study area, fixed receiver arrays can be used to detect out-migration so that those fish can be censored from the analysis (and not incorrectly attributed to harvest).

This approach accounts for relocations of live fish and natural mortalities and allows for relocation probabilities less than one (Hightower et al. 2001). Model assumptions are as follows: (1) every marked animal present in the study area at time i (whether alive or dead due to natural causes) has the same probability of being relocated on the ith search occasion; (2) every marked animal alive and in the study area at time i has the same probability of surviving to the next search occasion; (3) the probability of transmitter failure or of a transmitter being shed is negligible; (4) all animals behave independently with respect to relocation and survival probabilities; (5) fish that leave the study area are either harvested or, if emigrating, are detected and censored; (6) a fish located repeatedly at the same site represents a natural or catch-and-release mortality; (7) natural mortality occurs immediately prior to the first relocation at the final site occupied by that fish; and (8) marked and unmarked animals are assumed to have equal survival rates.

Telemetry estimates of mortality rates have been produced for three reservoir populations of striped bass (Hightower et al. 2001; Young and Isely 2004; Thompson et al. 2007). The mortality estimates were generally precise and varied strongly among seasons. The seasonality of fishing can be important because of the high catch-and-release mortality observed when water temperatures are high (Wilde et al. 2000; Bettinger et al. 2005, Bettinger and Wilde 2013). A great benefit of these studies is the estimation of natural mortality, which is a parameter very hard to estimate any other way. Information about *F* versus *M* is helpful for understanding which source of mortality has a greater impact on abundance and the age or size distribution of the population. In these three examples, fishing mortality was substantially higher than natural mortality, suggesting that limits on harvest and catch-and-release mortality would produce more trophy-sized fish. Telemetry results can provide the information needed for yield modeling, for example, to examine different minimum size limits (Thompson et al. 2007).

Conventional tags only provide information at the times of tagging and recapture, whereas telemetry tags can provide information on multiple search occasions. Seasonal locations of sonic- or radio-tagged fish provide insights into habitat use (including summer refugia), spawning sites, and areas used for foraging. Telemetry locations can also aid in understanding habitat-related natural mortalities and spatial patterns in fishing. For example, all natural mortalities of telemetered striped bass in J. Strom Thurmond Reservoir occurred in mid to late summer in an area of unsuitable summer habitat (Young and Isely 2004). Fishing mortalities were concentrated in late spring and late summer in and around the tailrace of the next upstream dam (Young and Isely 2004).

A limitation of the telemetry approach is that it is not possible to distinguish between natural mortality and other sources of mortality that result in a stationary transmitter within the reservoir. The most likely cause would be mortality due to catch-and-release fishing, but another possibility would be for a fish to be filleted in the field, with the carcass (and transmitter) discarded in the water. These potential biases have not been a practical concern to date because the estimated *M*s in previous telemetry studies of reservoir striped bass have been quite low (suggesting that other causes of stationary transmitters were negligible). It may be worth examining the spatial pattern of natural mortalities in order to assess the potential for these sources of bias. If apparent natural mortalities of telemetered fish are concentrated in areas of high fishing activity, then catch-and-release mortality or discarding of carcasses may be a nonnegligible fraction of the estimate of *M*.

One design issue to consider is whether a telemetered fish should also be given an external tag. External tags can provide some additional biological data and might be necessary in order to recover archival tags (Thompson et al. 2007). For estimating mortality, a reported external tag can clarify the fate of a fish that disappeared from the study area, for example, whether the transmitter failed, the fish was harvested, or the fish emigrated undetected and was caught (whether released or harvested) outside the study area. This information is useful but difficult to use in a quantitative way because of the typically high rates of underreporting. Hightower et al. (2001) recommended against use of an external tag because it might affect an angler's decision about whether to harvest or release a fish.

Combining Conventional Tags and Telemetry

We believe that the most cost effective strategy for a tag-return study would be a combination of conventional tags (e.g., internal anchor) and telemetry. Conventional tags have the advantage of allowing large sample sizes because of the low cost of tags. Another advantage is that relatively little effort is required other than at times when tagging occurs. These tags provide direct information about fishing mortality (through the return of tags) but only indirect information about natural mortality. In contrast, telemetry tags are expensive so most studies are carried out with small sample sizes. Considerable effort is required to search the entire study area during each period (e.g., monthly), but as noted above, this provides reliable seasonal information about mortality in addition to ecological information. Telemetry provides direct information about natural mortality (telemetered fish that stop moving) but only indirect information about fishing (through the disappearance of transmitters).

The combined method requires the independent release of fish with conventional tags (e.g., internal anchor) and transmitters. As the two tag types have complementary strengths, the combined analysis may produce better estimates of fishing and natural mortality than either method alone (Pollock et al. 2004). It also provides a reliable estimate of the reporting rate for conventional tags without the need for auxiliary methods such as high-reward or planted tags. Another advantage is that combined estimates can be compared to estimates based only on conventional tags or only on telemetry. This is helpful in determining whether the two tag types are providing consistent information. One possible complication is that the conventionally tagged fish and the telemetry tagged fish may not always be monitored over the same spatial scales, so they may not be subjected to the same mortality forces over the whole course of the study, leading to inconsistent estimates. However, even in such cases, the two different estimates of natural mortality could provide very useful information. There could also be violations of assumptions for one or both tag types (e.g., if there was unexpected shedding of conventional tags, or transmitter failure). Bacheler et al. (2009) used the combined method on estuarine red drum *Sciaenops ocellatus* and found similar temporal patterns in fishing mortality but moderate differences in magnitude. Conventional tags in that study were applied over a much larger region than the telemetry study area, so differences in fishing or natural mortality could have been due to spatial differences in mortality rates. As in the simulations by Pollock et al. (2004), the results for red drum showed that information on natural mortality was obtained mostly from telemetry, whereas conventional tags provided most of the information about fishing mortality.

Conclusions

Much of the information needed for effective management of inland striped bass can be obtained through tagging studies. Abundance can best be estimated through tag-recapture methods, either using research sampling alone or in combination with angler catches. A short-term study is preferable so that population closure can be assumed. It can be difficult to generate adequate sample sizes in the large systems where inland striped bass generally occur, so it is valuable to conduct simulation studies prior to the start of field work to determine if expected sample sizes will provide acceptably precise results.

A tag-return study is a practical approach for estimating mortality rates of reservoir striped bass. It is critical to build in auxiliary studies to estimate potential biases such as tag loss, mortality due to tagging, and tag-reporting rate. Simulation studies done prior to the start of field work can assess the likely precision of study results, given planned sample sizes. The simulations could include the potential impact of factors such as nonreporting or tag loss, both of which reduce the sample size of returned tags. The best approach for separating total mortality into component rates F and M is to combine release of a large annual sample of conventional tags with a smaller release of telemetry-tagged fish. Tag-return estimates of F and M can also be used, in conjunction with a creel survey estimate of harvest, to estimate population size for harvestable fish.

An estimate of adult striped bass population size, whether generated through a tag-recapture or tag-return study, would be helpful in assessing the effectiveness of a stocking program. For populations dependent on stocked juveniles, the estimate of adult abundance could also be used to estimate survival over the difficult-to-study stage between juvenile and adult. Other management questions such as optimal stocking rate or striped bass impacts on prey species (e.g., Cyterski et al. 2002) could be answered effectively with the information produced through a tagging study.

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APPENDIX A. SURVIV code for simulating a tag-return experiment, with 3 years of releases of 200 fish per year and 5 years of returns. Cell probabilities are obtained from a standard Brownie model (model estimates survival and tag-recovery rates), with survival assumed to be constant for simplicity. Tag recovery values (cell frequencies) are determined in the simulations and are set at 0 except for the final cell, which is set equal to the number released.

```
PROC MODEL NPAR=6 ADDCELL /* From Brownie et al. (1978), p 21 */ ;
 COHORT = 200         /* Tagged yr 1 */ ;
   0:S(2)             /* Tags recovered yr 1 */ ;
   0:S(1)*S(3)        /* Tags recovered yr 2 */ ;
   0:S(1)**2*S(4)   /* Tags recovered yr 3 */ ;
   0:S(1)**3*S(5)   /* Tags recovered yr 4 */ ;
  200:S(1)**4*S(6)   /* Tags recovered yr 5 */ ;
 COHORT = 200         /* Tagged yr 2 */ ;
   0:s(3)             /* Tags recovered yr 2 */ ;
   0:s(1)*s(4)        /* Tags recovered yr 3 */ ;
   0:s(1)**2*s(5)       /* Tags recovered yr 4 */ ;
  200:s(1)**3*s(6)       /* Tags recovered yr 5 */ ;
 COHORT = 200         /* Tagged yr 3 */ ;
   0:s(4)             /* Tags recovered yr 3 */ ;
   0:s(1)*s(5)             /* Tags recovered yr 4 */ ;
  200:s(1)**2*s(6)             /* Tags recovered yr 5 */ ;
 LABELS;
   s(1)=Survival;
   s(2)=Tag-rec_rate_1;
   s(3)=Tag-rec_rate_2;
   s(4)=Tag-rec_rate_3;
   s(5)=Tag-rec_rate_4;
   s(6)=Tag-rec_rate_5;
PROC SIMULATE NSIM=100 SEED=4567555 ERROR TEST ;
INITIAL /* Statements that follow fix the true values for simulation */;
  s(1)=0.4;
  s(2)=0.4;
  s(3)=0.5;
  s(4)=0.4;
  s(5)=0.5;
  s(6)=0.4;
PROC ESTIMATE;
INITIAL /* Statements that follow fix the starting values for estimation */;
  s(1)=0.5;
  s(2)=0.5;
  s(3)=0.5;
  s(4)=0.5;
  s(5)=0.5;
  s(6)=0.5;
```