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Improving Inferences from Fisheries Capture-Recapture Studies through Remote Detection of PIT Tags

The Challenges of Tracking Habitat Restoration at Various Spatial Scales

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COVER: A box housing PIT tag readers and associated equipment is mounted on a platform amidst spawning Lost River suckers (*Deltistes luxatus*) at Sucker Spring, Upper Klamath Lake.
CREDIT: U.S. Geological Survey.

FEATURE:
FISHERIES RESEARCH

Improving Inferences from Fisheries Capture-Recapture Studies through Remote Detection of PIT Tags

Lost River sucker (*Deltistes luxatus*)

TUPPER BLAKE, U.S. FISH AND WILDLIFE SERVICE

ABSTRACT: Models for capture-recapture data are commonly used in analyses of the dynamics of fish and wildlife populations, especially for estimating vital parameters such as survival. Capture-recapture methods provide more reliable inferences than other methods commonly used in fisheries studies. However, for rare or elusive fish species, parameter estimation is often hampered by small probabilities of re-encountering tagged fish when encounters are obtained through traditional sampling methods. We present a case study that demonstrates how remote antennas for passive integrated transponder (PIT) tags can increase encounter probabilities and the precision of survival estimates from capture-recapture models. Between 1999 and 2007, trammel nets were used to capture and tag over 8,400 endangered adult Lost River suckers (*Deltistes luxatus*) during the spawning season in Upper Klamath Lake, Oregon. Despite intensive sampling at relatively discrete spawning areas, encounter probabilities from Cormack-Jolly-Seber models were consistently low (< 0.2) and the precision of apparent annual survival estimates was poor. Beginning in 2005, remote PIT tag antennas were deployed at known spawning locations to increase the probability of re-encountering tagged fish. We compare results based only on physical recaptures with results based on both physical recaptures and remote detections to demonstrate the substantial improvement in estimates of encounter probabilities (approaching 100%) and apparent annual survival provided by the remote detections. The richer encounter histories provided robust inferences about the dynamics of annual survival and have made it possible to explore more realistic models and hypotheses about factors affecting the conservation and recovery of this endangered species. Recent advances in technology related to PIT tags have paved the way for creative implementation of large-scale tagging studies in systems where they were previously considered impracticable.

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Mejoramiento de las inferencias obtenidas en estudios de captura-recaptura mediante detección remota de marcas internas

RESUMEN: En los análisis de dinámica poblacional de peces y poblaciones naturales es común utilizar los modelos de captura-recaptura, especialmente para estimar parámetros clave como la supervivencia. Los métodos de captura-recaptura brindan estimaciones más confiables que otros métodos frecuentemente utilizados en estudios pesqueros. No obstante, para especies de peces raras o particularmente elusivas, la estimación de los parámetros a veces es afectada por la baja probabilidad de reencuentro de peces marcados cuando éste se basa en métodos tradicionales de muestreo. Se presenta un caso de estudio que demuestra cómo las antenas remotas para marcas electromagnéticas internas (PIT tags) pueden incrementar la probabilidad de encuentro y la precisión de las estimaciones de supervivencia derivadas de los modelos de captura-recaptura. Entre 1999 y 2007, mediante una red de trasmallo, se capturaron 8,400 individuos adultos del matalote (*Deltistes luxatus*) durante la época reproductiva en el Lago Upper Klamath, Oregon. A pesar de haber realizado un intenso muestreo en zonas de reproducción relativamente bien delimitadas, las probabilidades de encuentro calculadas con los modelos Cormack-Jolly-Seber fueron consistentemente bajas (< 0.2) al igual que la precisión de las estimaciones de supervivencia anual. Al inicio de 2005, se colocaron antenas remotas en sitios conocidos de reproducción para rastrear marcas electrónicas internas y aumentar las probabilidades de reencuentro de los peces marcados. Con el fin de demostrar una mejora sustancial en las estimaciones de las probabilidades de encuentro (cerca del 100%) y de la supervivencia anual que se obtienen utilizando detección remota, se compararon los resultados tanto sobre la base de individuos recapturados como de individuos recapturados y detecciones remotas. El grupo de datos con un mayor número de reencuentros sirvió para hacer inferencias más robustas acerca de la dinámica anual de la supervivencia e hizo posible explorar modelos más realistas e hipótesis sobre los factores que afectan a la conservación y recuperación de esta especie amenazada. Los avances tecnológicos recientes relacionados a las marcas electrónicas internas, han preparado el camino para implementar estudios de marcado a gran escala en sistemas en los que dichos trabajos se consideraban impracticables.

INTRODUCTION

Management and conservation of animal populations depend on an understanding of key life history parameters and their roles in regulating population dynamics. For example, populations of fish species with low natural survival rates are often more productive and can support more intense exploitation than species with higher natural survival rates (Adams 1980). Such populations are said to be evolutionarily adapted to low survival and compensate through rapid growth or high fecundity. For long-lived species with high natural survival rates, populations can be rapidly depleted by harvest and other sources of anthropogenic mortality (Fujiwara and Caswell 2001), and population growth rates are sensitive to variability in survival (Pfister 1998; Doherty et al. 2004; Schmutz 2009). In some situations, populations of imperiled species may require intervention to increase or stabilize survival and reduce the risk of extinction.

Accurate and precise estimates of survival are needed to evaluate hypotheses about factors that influence population dynamics and to develop effective management strategies. Capture-recapture (CR) or tagging studies are arguably the most reliable methods for generating such estimates, and development of theory and methods for analysis of CR data has been exceptionally rapid in the past few decades (Seber and Schwarz 2002; Senar et al. 2004; Thomson et al. 2009). Researchers are now able to use CR data to directly evaluate factors affecting not only survival (Burnham et al. 1987; Lebreton et al. 1992; Nichols 2005), but also recruitment and population growth rate (Pradel 1996; Nichols et al. 2000; Nichols and Hines 2002), movement or migration (Schwarz and Arnason 1990; Schwarz et al. 1993; Schwarz 2009), and reproductive success (Nichols et al. 1994; Rotella 2009). Most recent developments can be viewed as special cases of a flexible class of models that treat individual animals as occupying one of a number of states, broadly defined, in any given time period (Lebreton and Pradel 2002; White et al. 2006; Bailey et al. 2009; Kendall 2009).

Borrowing theory and methods from generalized linear models, CR models can incorporate and evaluate the effects of variables (covariates) on model parameters, permitting evaluation of interesting biological hypotheses (Lebreton et al. 1992; Franklin 2001; Bonner and Schwarz 2004; Nichols 2005; Cam 2009; Conroy 2009). Models can be fit by maximum likelihood with free software, and competing models that represent various hypotheses can be compared in a model selection framework (White and Burnham 1999; Choquet et al. 2004). Importantly, a model selection framework avoids inappropriate interpretations of classical statistical tests as strength of evidence (Royall 1997), leads to a parsimonious interpretation of the data as represented by models, and provides a means to account for model selection uncertainty in estimates of model parameters and their variances (see Chatfield 1995 and Buckland et al. 1997; part of multimodel inference sensu Burnham and Anderson 2002 and Anderson 2008).

Capture-recapture data have been and remain integral to studies of fish stocks in marine and coastal ecosystems, most often in the form of tag returns from fishermen that are used in stock assessment analyses. Despite all of the advantages of CR, freshwater fisheries researchers have been slow to include CR studies and modern methods of analysis in their toolbox for estimating survival and other demographic parameters (Pine et al. 2003). Perhaps the primary reason for the tepid response is that fisheries capture-recapture studies are often difficult to implement. Three concerns are commonly expressed:

1. Cost and effort associated with tagging and recapture sampling is prohibitive;
2. Statistical model assumptions about tag retention and the effects of tagging on behavior and survival are hard to meet; and
3. Capturing and tagging a subset of fish that can be considered representative of the population as a whole is difficult.

We suggest that the first two concerns about costs and model assumptions can usually be overcome by careful planning and design, and that the benefits to inference about population dynamics from CR studies outweigh the costs. Tag retention and effects of tagging can be assessed with pilot or complementary studies, although a reliable tagging method with minimal adverse effects remains a prerequisite for robust inference. Fortunately, a large body of literature is available on tag types and tagging techniques for fishes (Parker et al. 1990; Nielsen 1992; Guy et al. 1996), as well as design and analysis of CR studies (Burnham et al. 1987; Pollock et al. 1990; Williams et al. 2002).

Concerns about the representativeness of the tagged subset of fish are important, but they should not prohibit important inferences from being made in most cases. Representative sampling is important for inferences based on CR, as it is for any statistical analysis of sample data. However, most fisheries studies require CR models that are applicable to open populations; that is, those that undergo change due to births, deaths, or migration during the study period. Inferences about dynamics in open populations can be restricted to the tagged subset of fish using models of the Cormack-Jolly-Seber (CJS) type (Lebreton et al. 1992). The CJS models are conditioned only on the encounter histories of tagged fish; as a result, CJS models avoid the numerous pitfalls associated with estimating population size (reviewed in Cormack 1968 and Williams et al. 2002, which contrast with Hayes et al. 2007). Because formal statistical inference is restricted to the tagged fish, generalization of inferences from CJS models to the population as a whole must be based on the adequacy of the study design. Provided that tagged fish are reasonably similar to the rest of the population, results should be useful in quantifying dynamics and evaluating hypotheses. Scientific inference is a process, and sampling and modeling can always be adapted to address important sources of variation that are expected or discovered in the population, such as those that might affect the representativeness of the tagged subset of fish.

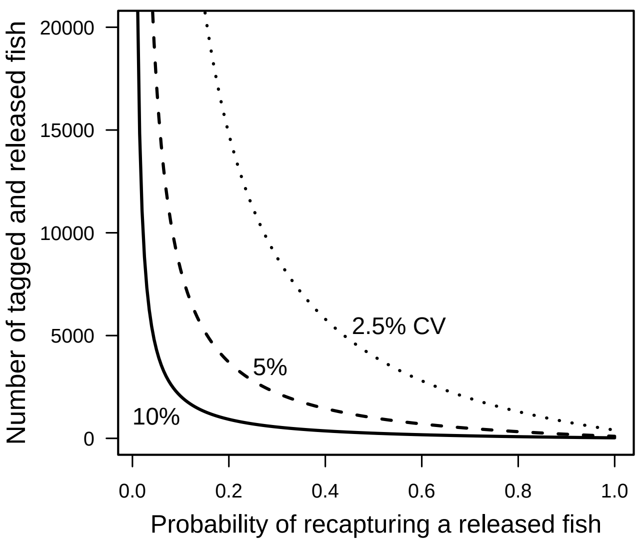
A lingering and critical limitation for CR studies of fish populations is the need for relatively high probabilities of re-encountering tagged fish. High encounter probabilities are essential for estimating parameters of interest with satisfactory precision and, of equal or greater importance, for evaluating model assumptions (Cormack 1968; Burnham et al. 1987; Lebreton et al. 1992). Unfortunately, recapture probabilities for tagged fish are often low in large water bodies, including many lakes and rivers and most estuarine and marine systems, and enormous sample sizes are needed to make inferences in such situations (e.g., Jiang et al. 2007). Low recapture probabilities are particularly common when the population is diffuse or the species is otherwise difficult to capture with traditional gears. The trade-off between encounter probabilities and sample size in study design has led to what is known as the "big law" of CR—increase encounter probabilities by any means possible (Figure 1). As a general guideline, encounter probabilities should be 0.2 or higher for modeling and inference to be fruitful without unreasonable sample sizes.

In this article, we describe the development of a capture-recapture monitoring program for endangered Lost River suckers (*Deltistes luxatus*) in which we had to overcome the problem of low encounter probabilities. Intensive sampling with traditional gears was unable to provide sufficient recaptures of fish tagged with passive integrated transponder (PIT) tags, but creative use of remote antennas increased encounter probabilities to nearly 100% and provided more robust model-based inferences about population dynamics. We suggest that recent advances in technology for PIT tags and antennas have made it possible to overcome the problem of low encounter probabilities in many systems, thus allowing for the implementation of capture-recapture studies in situations where they were previously considered impracticable.

Figure 1. An example of the "big law" of capture-recapture studies—increase encounter probabilities by any means possible. The example is based on a simple treatment-control experiment to estimate the effect of dam turbine passage on survival, and is based on the equation in Burnham et al. (1987:315). The effect size (*E*) is the ratio of survival for the treatment group to survival for the control group, and is set to 0.8, representing a 20% reduction in survival due to passing through the turbine. The study is a true experiment and the two groups of fish are assumed to be identical except for their probability of survival. The total required number of tagged and released fish, divided equally among treatment and control groups, is plotted against the probability of recapturing a released fish for three target values of the coefficient of variation (CV) for the estimated effect size: 2.5%, 5%, and 10%

$$[CV(\hat{E}) = \frac{se(\hat{E})}{\hat{E}} \times 100]$$

Increasing the probability of recapturing a tagged and released fish yields strongly disproportionate reductions in the required number of fish that need to be tagged to achieve a given level of precision on the effect size.



STUDY SPECIES AND SYSTEM

Lost River suckers are long-lived catostomids endemic to the Upper Klamath River Basin in Oregon and California (Miller and Smith 1981; Scoppettone and Vinyard 1991). Individuals have been aged to over 40 years and the largest adult females can grow to 800 mm fork length (FL; Scoppettone 1988; Scoppettone and Vinyard 1991; Janney et al. 2008). Lost River suckers were listed as endangered under the U.S. Endangered Species Act in 1988 because of range contractions, declines in abundance, and a lack of evidence of recent recruitment to adult populations (USFWS 1988). Direct mortality from subsistence and recreational fisheries for spawning suckers may have contributed to population declines, but fishing for the suckers was banned in 1987 (USFWS 1993). Numerous other threats common to imperiled fishes in the western United States were identified as potentially contributing to the declines (e.g., habitat alteration and degradation, nonnative species), but the relative influence of the various causes is uncertain (NRC 2004).

The most intensively studied remaining population of Lost River suckers occurs in Upper Klamath Lake, Oregon (UKL). Two apparently distinct spawning subpopulations of Lost River suckers coexist in UKL (Janney et al. 2008). One subpopulation exhibits a reproductive strategy similar to other western lakesuckers (genus *Chasmistes*) and migrates relatively short distances up tributaries to spawn in the spring. Although spawning may have occurred in other tributaries in the past, nearly all riverine spawning activity for the suckers is now restricted to the lower Williamson River and the Sprague River (Figure 2). The other subpopulation spawns at upwelling springs along the eastern shore of the lake below Modoc Rim. The majority of spawning activity for both subpopulations occurs in March and April.

Impaired water quality conditions in Upper Klamath Lake have been implicated in reduced survival of adult suckers and are a concern for recovery efforts. Upper Klamath Lake is the largest lake in Oregon (280 km^2), but is relatively shallow (aveage depth ca. 2 m). The combination of this bathymetry

U.S. GEOLOGICAL SURVEY

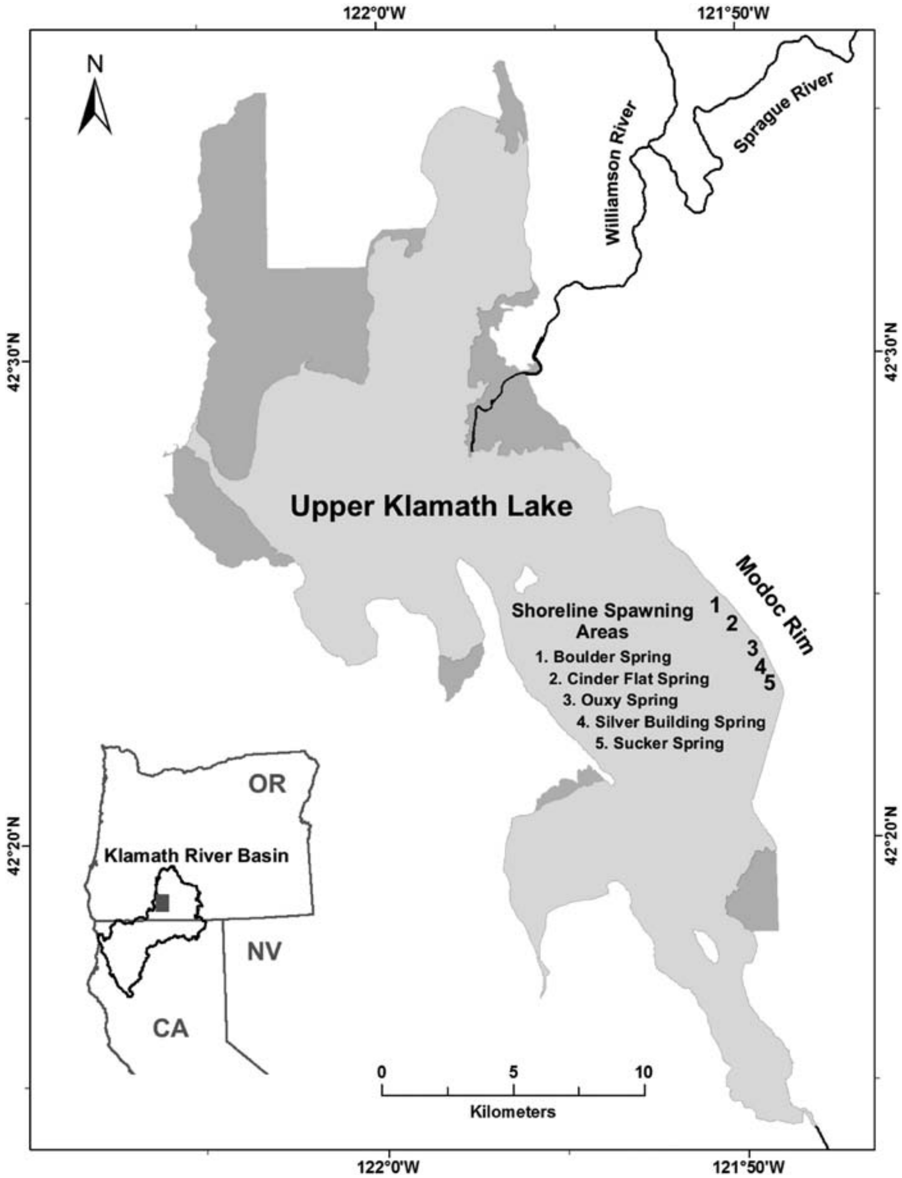


Figure 2. Map of Upper Klamath Lake showing the five spawning areas at springs along the eastern shoreline below Modoc Rim. Fringing marshes and other wetlands are shown in dark grey. The shaded area in the inset shows the location of the lake within the Klamath River Basin.

with a watershed naturally enriched in phosphorus has led to the conclusion that the lake has been eutrophic since the earliest records in the mid-1800s (NRC 2004; Kann and Welch 2005). However, water quality in UKL has been markedly altered from those historical conditions by various human activities in the watershed, particularly the drainage of marshes and wetlands, timber harvest, and water control and allocation related to agricultural development (Bradbury et al. 2004). These changes have created a hypereutrophic system that experiences massive phytoplankton blooms dominated by a single cyanobacterium, *Aphanizomenon flos-aquae* (Lindenberg et al. 2009). Phytoplankton blooms in the summer and fall are associated with direct and indirect mortality of adult suckers and can lead to large fish die-offs (Perkins et al. 2000).

METHODS

Capture, tagging, and encounters of tagged fish

Our capture-recapture program in Upper Klamath Lake has been ongoing since 1995 and focuses equally on adult Lost River suckers and co-occurring endangered shortnose suckers (*Chasmistes brevirostris*). However, for simplicity of presentation we only describe sampling and analysis methods for the subpopulation of Lost River suckers that spawns at the shoreline springs, and we only include fish tagged in 1999 and later. Fish encountered at the springs are rarely encountered elsewhere in our sampling, so focusing on the spring spawning subpopulation greatly simplifies description. More details of life history, sampling, and analysis for both species are given in Scoppettone and Vinyard (1991), NRC (2004), and Janney et al. (2008).

From 1999 to 2008 we captured Lost River suckers for tagging by setting trammel nets at five known spring spawning areas between February and May, beginning soon after ice-out (Figure 2). Nets were set twice per week at each spring, allowing three or four days between sampling events at a given spring. Sampling for the season was continued until only a few fish were captured in a given week. Trammel nets (30 m x 1.8 m; 29 cm bar outer mesh, 3.5 cm bar inner mesh) were deployed from shore by wading in a semicircle around the perimeter of the area of concentrated spawning. Spawning areas are relatively small; size varies among springs, but is typically 500 m^2 or less. Nets were deployed for four hours around sunset and checked at least once per hour for newly captured fish. Captured fish were retained in floating net pens for processing and were released when sampling was completed for the night. None of the fish died as a result of handling or retention in the net pens and all released fish appeared vigorous, so we consider short-term mortality associated with sampling to be negligible.

Captured fish were scanned for the presence of a PIT tag and untagged fish were injected with a tag using a hypodermic syringe with a 12-gauge needle. The PIT tags were injected into the abdominal musculature anterior to the pelvic girdle. All fish tagged prior to 2005 were given 12 or 14 mm 125.0 kHz full-duplex tags, and all fish tagged in 2005 and thereafter were given 12 mm 134.2 kHz full-duplex tags.

Physical recaptures of tagged fish were obtained from the trammel net sampling from 2000 to 2008, but the number of fish recaptured by this method was consistently low relative to the number of fish previously tagged and released (Table 1). In the spring of 2005, as an experimental approach to increase the probability of re-encountering tagged fish, we opportunistically deployed a single remote flat plate PIT tag antenna at Cinder Flat spring (Biomark, 30.5 x 66 cm; Figure 3). The antenna was deployed for parts of 10 days late in the spawning season, between 21 April and 6 May, yielding a total sampling time of approximately 135 hours. Beginning in 2006, we deployed flat plate antennas for the entire spawning season at four springs: Cinder Flat, Ouxy, Silver Building, and Sucker (Figure 2). Two or three antennas were used at each spring, and each antenna was connected to its own Biomark FS2001F-ISO reader by a 6-m cable. Readers were stored in metal boxes on fixed platforms near the middle of the spawning areas and antennas were distributed around the platforms (Figure 3).

Analysis and modeling

Inferences about adult Lost River sucker survival have benefited greatly from the encounters provided by the remote PIT tag antennas, and we illustrate the benefits by comparing results from two sets of Cormack-Jolly-Seber models. Comprehensive reviews of CJS models were provided by Seber (1982), Pollock et al. (1990), Lebreton et al. (1992), Williams et al. (2002), and Nichols (2005). The fundamental input to CJS models are the encounter histories (series of zeros and ones where the ones indicate an encounter on a given sampling occasion; e.g., 1000010111), and the parameters of interest are apparent survival probabilities (Φ) and encounter probabilities (p). Apparent survival includes true survival as well as permanent emigration from the study area, but in our case Φ closely approximates true survival because very few adult Lost River suckers leave Upper Klamath Lake (Banish et al. 2009).

Our first model set was developed for encounter histories that included only physical recaptures from trammel net sampling, and the second was developed for encounter histories that included both physical recaptures and remote encounters. Survival and encounter probabilities were estimated over annual time intervals, so multiple encounters of the same fish in the same sampling season (February-May) were treated as a single encounter. Model sets were developed by considering the effects of sex and time (year) on Φ and p, and then including models with and without those factors. We modeled Φ as a function of sex because we expected that greater reproductive investment by females would lead to lower survival compared to males. Most importantly, we modeled Φ as a function of time because we hoped to detect changes in annual survival and relate those changes to factors such as

Table 1. Summary of releases and re-encounters of PIT-tagged Lost River suckers in Upper Klamath Lake, Oregon between 1999 and 2008. The total annual re-encounters of tagged fish in 2000–2008 are shown at the top, for each encounter method separately (physical recapture with trammel nets [N] and detection on remote PIT tag antennas [R]) and in combination. Re-encounters for 2000–2004 include only recaptures from trammel nets; remote antennas were first used to a limited extent in 2005 (see text). Encounters for one method can include fish also encountered by the other method, so the combined encounters are lower than the sum of the per-method encounters. Re-encounters of fish in the year in which they were tagged are excluded from the counts. The remainder of the table is broken down by release cohort and shows the numbers of tagged fish from a cohort that were re-encountered for the first time in a given year. In this part of the table, successive columns include only fish that were never previously re-encountered, by either physical recapture or remote detection, and remote columns exclude fish that were also recaptured in nets.

ANNUAL RE-ENCOUNTERS OF TAGGED FISH

	2000	2001	2002	2003	2004	2005		2006		2007		2008	
						N	R	N	R	N	R	N	R
Total re-encounters by type	51	152	219	341	383	500	157	182	4,787	471	4,766	345	5,078
Total re-encounters combined	51	152	219	341	383	642		4,794		4,792		5,092	

FIRST RE-ENCOUNTERS OF TAGGED FISH

Release cohort	Number released	2000	2001	2002	2003	2004	2005		2006		2007		2008		Individuals encountered again	Individuals never encountered again
							N	R	N	R	N	R	N	R		
1999	744	51	52	34	44	44	18	15	7	181	1	17	0	4	468	276
2000	1,056		91	75	70	46	49	23	17	308	1	24	0	3	707	349
2001	1,262			82	99	68	71	0	17	422	7	53	3	13	835	427
2002	983				74	57	51	0	13	390	6	10	0	0	601	382
2003	1,343					79	83	57	22	753	4	26	2	7	1,033	310
2004	979						82	30	17	665	3	38	1	7	843	136
2005	1,017								27	899	1	6	0	2	935	82
2006	369										30	310	1	5	346	23
2007	698												28	605	633	65
Total	8,451	51	143	191	287	294	354	125	120	3,618	53	484	35	646	6,401	2,050

water quality conditions. For p, we expected sex to be important because of differences in reproductive behavior (e.g., males stay at spawning areas longer than females, potentially increasing their probability of being encountered), and we expected time to be important because of annual differences in sampling intensity and environmental effects on the condition of the spawning habitat. Past analyses showed that models with some combination of both sex and time effects on p were overwhelmingly supported in model selection, so we only considered models with some combination of both effects (Janney et al. 2008). We included models with both additive and interactive effects for Φ and p. Additive models constrained effects to be the same between groups across time (e.g., the difference between male and female survival is the same in each year), whereas interactive models included more parameters and allowed effects to vary through time (e.g., separate estimates of survival for each sex in each year). Note that the last estimates of Φ and p are confounded in the likelihood and cannot be separately estimated; this is a general characteristic of CJS models. As such, we do not report or discuss estimates of Φ for 2007 or p for 2008.

The two model sets were the same with one important exception: the model set for the encounter histories that included remote detections incorporated models with an effect of PIT tag type (125.0 vs. 134.2 kHz) on encounter probability in 2006–2008. The 134.2 kHz tags were first used in 2005 and first re-encountered in our 2006 sampling. The higher frequency tags have a greater read range and are more likely to be detected on the remote antennas than lower frequency tags. In our application, the distance from the antennas at which the 134.2 kHz tags can be read is 15–20 cm, compared with 5 cm for the 125.0 kHz tags. We included models that constrained the effect of tag type to be the same in 2006, 2007, and 2008, as well as models that allowed the effect of tag type to vary by year.

We used program MARK to fit the models using maximum likelihood (White and Burnham 1999). Models were specified and passed to MARK using the RMark package (Laake 2009; Laake and Rexstad 2009) within the R software environment (R Development Core Team 2009). All model likelihoods were constructed using a logit link function and optimized using the default Newton-Raphson algorithm.

Models within a set were compared using an information-theoretic model selection framework and Akaike's Information Criterion corrected for small sample size and overdispersion (*QAIC*c; Burnham and Anderson 2002). For each model in a set, we follow Anderson et al. (2001) and report five quantities:

Figure 3. Clockwise from top left: a remote flat plate PIT tag antenna on the substrate; a box for housing the PIT tag readers and associated equipment, mounted on a platform amidst spawning suckers at Sucker Spring; an underwater photograph of spawning Lost River suckers.

1. The number of estimated parameters (k),
2. $QAICc$,
3. The difference in $QAICc$ between a given model and the Kullback-Leibler (K–L) best model in the set ($\Delta QAICc$),
4. The probability that the model is the best K–L model in the set (model probability, or Akaike weight, w_i), and
5. The value of the maximized log-likelihood function ($-2log_eL$).

Evidence ratios are used to compare pairs of models and are simply the ratio of model probabilities. Where possible, we account for model selection uncertainty in parameter estimates by calculating estimates and estimated variances as weighted averages from all models in the set, using the model probabilities as weighting factors.

Assumptions of the Cormack-Jolly-Seber model

The CJS model makes the following assumptions:

1. Tags are not lost, or missed when individuals are re-encountered;
2. Sampling periods are "instantaneous" relative to the interval between samples; and
3. There is no unmodeled individual variability (heterogeneity) in survival or encounter probabilities among the tagged animals.

Assumptions 1 and 2 must be addressed primarily through study design. For Lost River suckers, double-tagging experiments with Floy and PIT tags showed that PIT tag loss rates were less than 1% over three or more years (U.S. Geological Survey, unpublished data). For physical recaptures, we ensured that tags were not missed when present by scanning a test tag prior to scanning each fish, and also scanning a test tag after each fish that was found to be untagged. Regarding Assumption 2, sampling in our study occurs over a 3 to 3.5 month spawning period and is not instantaneous. However, the vast majority of captures and remote encounters occur over a much shorter time period, and individuals are fairly consistent from year to year in the relative times at which they join the spawning aggregation. Thus, on an individual basis, sampling can be considered nearly instantaneous relative to an annual interval used for parameter estimation. In addition, spawning fish almost always appear to be in excellent condition and water quality is good during the spring. Thus, we expect that little mortality occurs during the sampling period and does not bias survival estimates.

Assumption 3 regarding heterogeneity is complex and has received considerable attention in the capture-recapture literature (reviewed in Pollock et al. 1990; Williams et al. 2002; Pollock and Alpizar-Jara 2005). This assumption includes the important and well-recognized requirement for negligible effects of tagging on survival. Our observations of Lost River suckers after tagging suggest that mortality related to handling and tagging is negligible, but future analyses will investigate this further. Other aspects of Assumption 3 are often not fully addressed or are completely ignored in fisheries studies (Pine et al. 2003). One of the primary advantages of CJS models is that estimates of apparent survival are robust to heterogeneity in encounter probabilities (Carothers 1973; Gilbert 1973; Carothers 1979). Nonetheless, unmodeled heterogeneity in encounter probabilities will likely remain of concern in most large-scale fisheries capture-recapture studies, and we return to this issue in the Discussion. Heterogeneity can be addressed to some extent through goodness-of-fit testing and correction for overdispersion (Lebreton et al. 1992; Burnham and Anderson 2002). We performed goodness-of-fit tests for the most general model in each model set and neither showed any consistent departure from expectations under the CJS model (see also Janney et al. 2008). However, a small amount of overdispersion was evident, presumably caused by a lack of independence in the fates of tagged fish, and we corrected model selection statistics and inflated parameter variances to account for the overdispersion using a variance inflation factor ($\hat{c}$). We estimated $\hat{c}$ with the median $\hat{c}$ procedure in program MARK.

RESULTS

Summary of capture, tagging, and encounters

Between 1999 and 2007, 8,451 adult Lost River suckers were captured and tagged at the spring spawning areas (Table 1). We recaptured 2,005 of those individuals (24%) in subsequent trammel net sampling through 2008. However, recaptures of tagged fish in a given year were low considering the intensity of our sampling and the discrete distribution of spawning activity. Trammel net recaptures never exceeded 500 individuals in a given year.

In contrast, by including the detections of fish on remote PIT tag antennas in 2005–2008, we re-encountered 6,401 of the tagged individuals (76%) and total annual re-encounters increased dramatically (Table 1). In the absence of detections from the remote antennas, 4,396 tagged fish were available in the population but would not have contributed to our inferences about survival. In 2005 alone, when a single antenna was deployed for a short period late in the spawning season at one spawning area, we detected 157 individuals that had been tagged prior to 2005, which compares with 500 individuals recaptured in trammel nets over five spawning areas throughout the 3-month spawning season. Of the 157 fish detected remotely, 125 had not been previously recaptured in trammel nets despite being at large for as many as 6 years (Table 1). In 2006, the first year of full remote antenna implementation, we detected 4,787 individuals over the course of the spawning season, compared to 182 individuals recaptured in trammel nets. Of the remotely detected fish, 3,618 had never been re-encountered before by either method. Even in 2008, after two years of full remote antenna coverage and eight years of trammel net sampling, four individuals that had been tagged in 1999 were re-encountered for the first time only on the remote antennas.

Analysis including only physical recaptures

Model selection results and parameter estimates indicated that the data set that included only physical recaptures could support rather limited inferences about annual survival of PIT-tagged Lost River suckers. The top model, which had a

0.935 probability of being the Kullback-Leibler best model in the set, included additive effects of sex and time on Φ and the same additive structure for *p* (Table 2). The second best model included the same additive structure for *p* but separate estimates of Φ for each sex in each year; this model had much less support (Δ*QAIC*c = 5.8, model probability = 0.051). The only difference between this model and the top model was the structure on Φ, so the evidence ratio between the two models, 18.3, is direct and fairly strong evidence in support of additive structure on Φ. All other models, including the global model [model 9; Φ(sex*time), *p*(sex*time)], had essentially no support (Δ*QAIC*c > 10, evidence ratios compared to the top model > 150).

Estimates of Φ from the top model were imprecise, particularly for males, and the point estimates for both sexes in 2000 and 2001 were on a boundary (1.0; Figure 4). The boundary estimates indicate that the data provided insufficient information to the likelihood in those years. In the second best model with full structure on Φ, the 2000 and 2001 point estimates for males were on a boundary and five of the eight estimable parameters for females were on a boundary. Combined with much wider confidence intervals for the female estimates, the bottom line is that few of the Φ estimates from this model were usable, despite it being the second best model in the set. Estimation problems aside, point estimates of survival probabilities from the top model appeared to be relatively high for both sexes in all years, consistent with expectations based on life history (Figure 4).

Ultimately, limitations to inference about survival from the data set with only physical recaptures could be traced back to the "big law" (Figure 1). Recaptures were sparse and estimated encounter probabilities were consistently very low, never increasing to more than 0.2 (Figure 5). Consistent with our expectations, encounter probabilities for male suckers were more than double the encounter probabilities for female suckers; female encounter probabilities never exceeded 0.05. Strong decreases in encounter probabilities for both sexes in 2006 were a result of temporarily reduced sampling effort.

Table 2. Model selection results for the set of 10 Cormack-Jolly-Seber models fit to the data set including only physical recaptures of PIT-tagged Lost River suckers. The number of parameters estimated in each model is indicated by *k*, and the estimate of the overdispersion parameter ($\hat{c}$) used in calculating adjusted model selection criteria (*QAIC*c) was 1.17.

Model number	Model	*k*	*QAIC*c	Δ*QAIC*c	Model probability (w_i)	$-2log_eL$
1	Φ(sex+time),*p*(sex+time)	19	16,571.3	0.0	0.935	19,327.3
2	Φ(sex*time),*p*(sex+time)	27	16,577.1	5.8	0.051	19,315.3
3	Φ(sex),*p*(sex*time)	20	16,581.8	10.5	0.005	19,337.3
4	Φ(sex+time),*p*(sex*time)	27	16,582.1	10.8	0.004	19,321.1
5	Φ(.),*p*(sex*time)	19	16,582.6	11.3	0.003	19,340.5
6	Φ(time),*p*(sex*time)	26	16,586.7	15.4	0.000	19,328.9
7	Φ(time),*p*(sex+time)	18	16,587.6	16.3	0.000	19,348.7
8	Φ(sex),*p*(sex+time)	12	16,587.7	16.4	0.000	19,362.9
9	Φ(sex*time),*p*(sex*time)	34	16,588.5	17.2	0.000	19,312.2
10	Φ(.),*p*(sex+time)	11	16,600.0	28.7	0.000	19,379.6

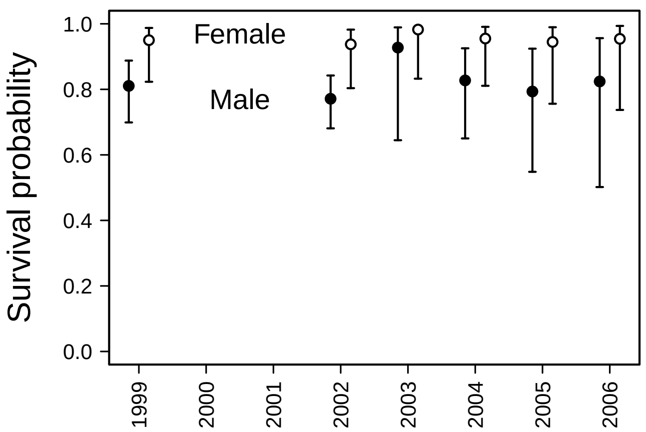


Figure 4. Estimates of survival probability (± 95% confidence intervals) from the top model [Φ(sex+time),*p*(sex+time)] in the set of models fit to the data set including only physical recaptures of PIT-tagged Lost River suckers. Estimates for both sexes in 2000 and 2001 are not shown because they were on a boundary (1.0), indicating estimability problems. Estimates were not model-averaged because of problems with boundary estimates, particularly in the second best model, but the top model received nearly all of the support (model probability = 0.935).

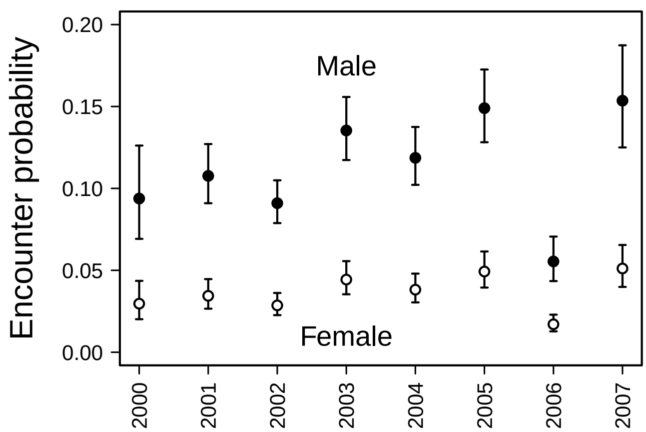


Figure 5. Model-averaged estimates of encounter probability (± 95% confidence intervals) from the set of models fit to the data set including only physical recaptures of PIT-tagged Lost River suckers. The estimate of the overdispersion parameter ($\hat{c}$) used in calculating adjusted standard errors was 1.17.

Analysis including all encounters

Model selection results and parameter estimates for the data set that included both physical recaptures and remote detections supported much stronger inferences about the dynamics of annual survival of PIT-tagged Lost River suckers. Similar to the model selection results for the data set that included only physical recaptures, the top two models in the set included additive effects of sex and time on Φ (Table 3). However, evidence ratios comparing models with additive versus full structure on Φ with the same structure on p were much more supportive of the full structure on Φ (model 1 vs. model 3 = 7.0; model 2 vs. model 4 = 2.5). As expected based on the increases in re-encounters provided by the remote antennas during 2006–2008, model selection strongly favored the inclusion of many effects on p. The top six models all included separate estimates of p for each sex in each year and at least one effect for tag type in 2006–2008. None of the models without some form of tag type effect had any support.

The additional encounters from the remote antennas provided substantial improvements in precision for the estimates of survival probabilities. Model-averaged estimates of Φ were highly precise for the expanded data set (Figure 6), with coefficients of variation never more than 4%. Estimates were so precise in the most recent years that survival probabilities were essentially known for the tagged set of fish. In contrast to the data set including only physical recaptures, survival probabilities for both sexes in 2000 were estimable, and both point estimates were near 1.0. However, point estimates for

Table 3. Model selection results for the top 10 Cormack-Jolly-Seber models fit to the data set including both physical recaptures and remote detections of PIT-tagged Lost River suckers. Twenty-five other reduced models were considered, but all had Δ*QAIC*c > 33 and are not shown. The "tagtype" effect on *p* in the model names refers to the difference between 125.0 kHz and 134.2 kHz tags, which is only included for the years 2006, 2007, and 2008 (see text). The tagtype effect is either constrained to be the same across years ("tagtype" alone) or allowed to vary by year ("tagtype*time"). Both structures were combined additively (+ precedes tagtype) and interactively (* precedes tagtype) with the other effects in the models. The number of parameters estimated in each model is indicated by *k*, and the estimate of the overdispersion parameter ($\hat{c}$) used in calculating adjusted model selection criteria (*QAIC*c) was 1.35.

Model number	Model	*k*	*QAIC*c	Δ*QAIC*c	Model probability (w_i)	$-2\log_e L$
1	Φ(sex+time),*p*(sex*time+[tagtype*time])	30	22,695.4	0.0	0.606	30,557.7
2	Φ(sex+time),*p*(sex*time+tagtype)	28	22,697.8	2.4	0.179	30,566.4
3	Φ(sex*time),*p*(sex*time+[tagtype*time])	37	22,699.3	3.9	0.088	30,543.9
4	Φ(sex*time),*p*(sex*time+tagtype)	35	22,699.6	4.2	0.076	30,549.7
5	Φ(sex+time),*p*(sex*time*tagtype)	33	22,700.6	5.2	0.044	30,556.6
6	Φ(sex*time),*p*(sex*time*tagtype)	40	22,704.6	9.2	0.006	30,543.0
7	Φ(sex+time),*p*(sex+time+[tagtype*time])	22	22,709.0	13.6	0.001	30,597.6
8	Φ(sex+time),*p*(sex+time+tagtype)	20	22,709.8	14.4	0.000	30,604.2
9	Φ(sex*time),*p*(sex+time+[tagtype*time])	29	22,712.6	17.2	0.000	30,583.5
10	Φ(sex*time),*p*(sex+time+tagtype)	28	22,715.4	20.0	0.000	30,590.1

Figure 6. Model-averaged estimates of survival probability (±95% confidence intervals) from the set of models fit to the data set including both physical recaptures and remote detections of PIT-tagged Lost River suckers. Estimates for both sexes in 2001 are not shown because they were on a boundary (1.0), indicating estimability problems. The estimate of the overdispersion parameter ($\hat{c}$) used in calculating adjusted standard errors was 1.35.

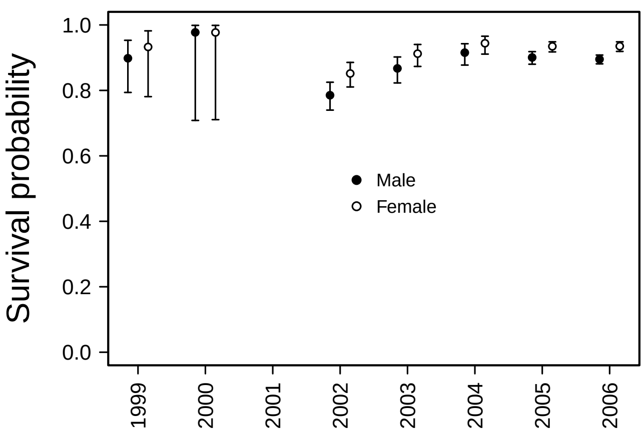
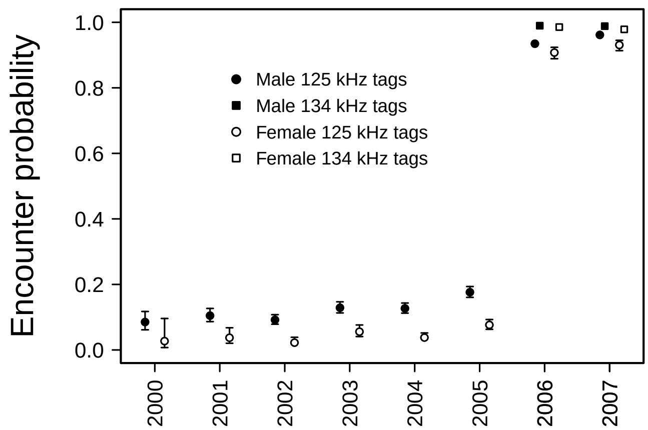


Figure 7. Model-averaged estimates of encounter probability (± 95% confidence intervals) from the set of models fit to the data set including both physical recaptures and remote detections of PIT-tagged Lost River suckers. The estimate of the overdispersion parameter ($\hat{c}$) used in calculating adjusted standard errors was 1.35. In 2006 and 2007, confidence intervals are only plotted for females with 125.0 kHz tags; for other estimates the confidence intervals are too narrow to distinguish them from the estimates [$se(\hat{p}) \leq 0.006$]. Note change in y-axis scale compared to Figure 5.



both sexes were again on a boundary (1.0) in 2001. Survival of PIT-tagged Lost River suckers in 2001 was either very nearly 100% or there was simply not enough information in the data about individuals at large during 2001; either explanation is plausible.

Compared to the estimates from the data set including only physical recaptures (Figure 4), point estimates of Φ based on the expanded data set changed by nontrivial amounts extending all the way back to 1999. Except for 2003, estimates for males increased by 1–11% when estimated with the expanded data set. Of particular note are the estimates for the three most recent years, which were all apparently underestimated by more than 7% using the data set with only physical recaptures. In contrast, Φ estimates for females decreased in each year by 1–9%, and the data set including only physical recaptures produced the largest apparent overestimations in 2002 and 2003. Estimates from both model sets indicated that female survival was greater than male survival in each year, in contrast to our expectations based on reproductive investment. Between 2002 and 2006, female survival ranged from 85 to 94% and male survival ranged from 79 to 92%.

The increased precision of the survival probabilities for the expanded data set derives almost entirely from the increased encounter probabilities in 2006 and 2007 (Figure 7). Although precision was better for encounter probabilities in all years using the expanded data set, point estimates were mostly unchanged through 2005, as expected. In contrast, encounter probabilities in 2006 and 2007 increased from 2–15% based on the data set with only physical recaptures to over 90% after including the remote detections. Encounter probabilities for fish with 134.2 kHz tags were 98% or greater, whereas encounter probabilities for fish with 125.0 kHz tags ranged from 91% to 96%. These results were consistent with our expectations that encounter probabilities would be higher for fish with the higher frequency tags. Put simply, when remote detections were included, tagged fish at large in the population were almost certain to be detected at some point during the spawning season.

DISCUSSION

Summary of findings

Remote detections of PIT-tagged Lost River suckers have improved the utility of capture-recapture methods for making inferences about population dynamics for this endangered species. Despite intensive sampling at relatively small, discrete spawning areas, probabilities of recapturing tagged suckers in trammel nets were low. Thus, in the absence of remote detections, the vast majority of individual encounter histories for tagged fish contained little information about survival because those fish were never re-encountered. The large proportion of uninformative encounter histories led to model selection results that favored simple structure on survival parameters. In addition, when compared to estimates based on all encounters, survival estimates were imprecise and apparently over- or underestimated by nontrivial amounts in a number of years. As a result, our capture-recapture data were not adequate to address important concerns about various factors potentially affecting the population dynamics and recovery of this species.

In 2006, 2007, and 2008, remote detections of PIT-tagged suckers that had never been previously re-encountered converted thousands of encounter histories from relatively uninformative strings of nondetections into information about encounter probabilities because uncertainty about survival of those fish in earlier years was eliminated. As a result, the data including the remote detections were highly informative for determining whether fish were alive and went undetected or had died. Estimates of both survival and encounter probabilities in the most recent years were so precise as to be essentially known.

Janney et al. (2008) showed that annual survival of adult suckers in Upper Klamath Lake was reduced in years when conspicuous fish die-offs occurred, but was also low in years without conspicuous fish die-offs. Those results add to ongoing concerns about the chronic effects of poor water quality and other sources of mortality on the recovery of endangered sucker populations (NRC 2004). The data provided by the remote detection systems has made it possible for us to pursue modeling that investigates hypotheses about the effects of various factors on survival. Results of such analyses are of pressing concern to management agencies tasked with conserving and recovering these species.

Remote detections and the "big law" of capture-recapture

Miranda and Bettoli (2007:251) noted that "tagging is not extensively used to assess mortality of fish populations, mostly due to cost and practical difficulties." Results from our PIT-tagging program have shown that it is possible to overcome one critical difficulty represented by the "big law"—low encounter probabilities—by use of remote detection systems. Capture probabilities are often very low for traditional fisheries gears, so the problem of low encounter probabilities will remain a hindrance to fishery-independent capture-recapture studies that rely on traditional gears. Capture probabilities can be increased by more intensive sampling or alternative sampling strategies, but costs can become prohibitive and some active gears may not be permissible for some species (e.g., electrofishing).

In an important sense, the encounter probability "problem" is also an advantage for fisheries CR studies, in that it requires investigators to confront the realities of sampling in the system. Capture-recapture studies will only provide robust inferences when the data provide substantial information about the animals under study, and low encounter probabilities and imprecise estimates make it clear that much remains unknown. Although this issue is raised most commonly for CR studies, it applies equally to any method that depends on capture data. Inferences based on samples that represent only a small percentage of the individuals in the population cannot be considered strong inferences.

Our results with remote detection systems for PIT tags should be encouraging to fisheries scientists considering CR methods and wrestling with the difficulties of low encounter probabilities. Although CR methods are often considered to be too expensive and too difficult to implement in fisheries studies, remote detection systems can shift the balance in their favor. Advances in technology have made it possible to construct antennas or arrays of antennas that can span entire rivers, up to 50 meters wide or wider. Antenna systems are now primarily restricted only by flow conditions in the study system (high flows or debris can damage antennas), and antennas often require only infrequent maintenance. In addition, the range at which tags can be read by the antennas continues to increase. Finally, data can be acquired and transmitted in a fully electronic and remote process, reducing or eliminating some sources of error.

The initial investment in establishing a capture-recapture program based on PIT tags and remote detections may be high, but costs decline substantially in subsequent years. The total equipment costs for full remote antenna implementation at our sites in 2006 was around $54,000 USD, but maintenance and supplemental costs in subsequent years have typically been less than $1,000. Under budget constraints, PIT-tagging efforts and remote detection systems can be developed incrementally by adding antennas and readers as funding allows. Encounter probabilities are estimated as part of the analysis, so these changes in sampling design can be accommodated in models and the precision of survival estimates will progressively improve. In most cases, once remote detection systems are in place and encounter probabilities increase, the number of fish that need to be tagged and released each year can be reduced, potentially reducing costs associated with field efforts. In addition, some equipment, including antennas, can be designed and assembled independently to save costs in comparison to purchasing proprietary equipment from commercial manufacturers.

Capture-recapture as an essential tool in fisheries

Freshwater fisheries scientists have been slow to appreciate the utility and advantages of capture-recapture methods for estimating survival and other demographic parameters, and also to adopt modern methods for analyzing CR data. On this count, we reiterate the advice of Pine et al. (2003) that CR methods have much to offer fisheries research and management. In turn, we concur with the recent synthesis concerning mortality estimation by Miranda and Bettoli (2007) that freshwater fisheries scientists should incorporate into their toolbox numerous methods that appear to be largely restricted to marine and coastal fisheries. We believe that modern CR methods are one such tool. The use of tagging studies and tag return data is increasing in analyses of marine and coastal fisheries. The challenges of implementing tagging studies in these large and open systems are greater than those for most freshwater systems (with the possible exception of some commercially exploited stocks), so the groundwork has been laid for implementing modern CR methods in freshwater fisheries.

Capture-recapture methods offer a number of advantages over traditional methods for estimating survival based on fishery-dependent catch and effort data or fisheries-independent survey data (e.g., catch curves, change-in-ratio methods, and length- or age-based methods; Ricker 1975; Hilborn and Walters 1992; Quinn and Deriso 1999). Most traditional methods provide estimates of survival that are notoriously imprecise and require strong assumptions that are difficult to meet or assess in order to avoid biased estimates (e.g., constancy of recruitment, survival, catchability, or growth). Indeed, many of the assumptions are known to be violated a priori, but are commonly ignored. Improvements to traditional methods, such as year-class curves (Cotter et al. 2007) and nonequilibrium length-based estimators (Gedamke and Hoenig 2006), can improve the accuracy and precision of survival estimates, but still require strong assumptions that are difficult to meet or assess. Furthermore, because studies of population dynamics are concerned with understanding variation in survival and the factors that influence it, the utility of many of the traditional methods is limited because they assume that survival is constant during the study.

In general, CR methods are designed to estimate many of the parameters that are "assumed away" in the traditional methods. For example, rather than make strong and untestable assumptions about the time-invariance of survival and encounter (recapture) probabilities to estimate a single survival rate, CR methods are designed to jointly estimate both parameters, and assumptions and temporal dynamics can be evaluated. As noted by D. G. Chapman (quoted in Cormack 1968:456):

> If far reaching assumptions are made, then strong conclusions are reached. But if these assumptions are not accepted then the whole structure built upon sand collapses.

Modern methods of CR analysis have been developed to accommodate the realities of fisheries and wildlife field studies, including heterogeneity in capture probabilities and failures of the closure assumption (Pollock 1982, 1991; Kendall et al. 1995; Williams et al. 2002; Pledger et al. 2003; Cowen and Schwarz 2006). These methods should be integrated into the standard toolbox of freshwater fisheries scientists.

Remaining hurdles

The advantages of remote detection systems to inference and estimation are numerous, but there are also limitations. Two of the thorniest issues in capture-recapture analyses are goodness-of-fit assessment and heterogeneity in encounter probabilities. Although the primary parameters of interest in CJS and related models (e.g., survival probabilities) are robust to heterogeneity in encounter probabilities (Carothers 1979; Pollock et al. 1990), model selection and inferential procedures become suspect when too much heterogeneity exists in the data. Such heterogeneity must be accounted for either by inflating variance estimates using a correction factor ($\hat{c}$) or by adding additional justifiable structure to the model. Given the nonrandom patterns of association among individual fish in many populations, heterogeneity in encounter probabilities is likely to be worse than in many wildlife studies (Pollock 1991; Seber and Schwarz 2002). No hard and fast rules exist, but $\hat{c}$ estimates above about 3.0 are suspicious and probably indicate that model structure is inappropriate (Choquet et al. 2009).

In our study, heterogeneity in encounter probabilities for Lost River suckers increased after the remote detection systems were put in place, and even more so after the change in the type of PIT tag (from 125.0 kHz to 134.2 kHz). Ironically, because encounter probabilities were so high, goodness-of-fit tests were very sensitive to small deviations from expected values. To address heterogeneity, we had to adjust model structures to account for the two different tag types and still had to account for overdispersion because some heterogeneity remained ($\hat{c}$ for data set with all encounters = 1.35). Encounter probabilities are typically not of primary interest ("nuisance" parameters), so effort should be directed at reducing heterogeneity to avoid using information in the data to estimate additional encounter probabilities.

An additional concern with remote detection systems is that they only detect the marked portion of the population. Information on the unmarked portion of the population is needed to estimate population size, recruitment, and population growth rate. Also, for models addressing hypotheses about individual covariates (e.g., length, weight, condition), individual fish must be captured for the covariate to be measured. Although modeling strategies are available to accommodate remote detections in some situations (e.g., Al-Chokhachy and Budy 2008), careful attention must be paid to study design and substantial effort will need to be directed at capture sampling when these additional parameters are of primary interest. In addition, new modeling strategies will be needed to accommodate some study situations.

Future possibilities

The technology of PIT tags has made it possible for researchers to routinely pursue biological questions that were nearly impossible to answer prior to the 1980s (Gibbons and Andrews 2004). Technological advances have continued to reduce the limitations of PIT tags for biological studies, and remote detection systems have further enhanced their utility (Prentice et al. 1990; Zydlewski et al. 2006). The data provided by remote detection systems opens up numerous possibilities for modeling and inference, allowing researchers to ask questions that address more complex hypotheses. For example, data from studies that previously were aimed at simply trying to obtain one estimate of survival can now be used to address hypotheses about factors affecting the dynamics of survival. The development of models to pursue such inferences has been the focus of much of the theoretical work in capture-recapture over the last decade (e.g., Thomson et al. 2009). Analyses will be more complex and challenging, but also more interesting from a biological standpoint.

Encounter data from remote detection systems should also allow capture-recapture methods to be used in systems where they were previously considered impracticable, from studies of rare or elusive species in small streams to assessments of fish populations in large systems. For rare or elusive fishes in small streams, physically recapturing tagged individuals with some reasonable probability may be impossible. However, a combination of surveys with portable detection systems (e.g., wands) and stationary antenna arrays operating continuously can be sufficient (Berger and Gresswell 2009). In large systems, such as Upper Klamath Lake, remote detection systems will need to target areas where individuals aggregate, such as spawning areas or constriction points in migration routes. For example, millions of fish are PIT-tagged in the Columbia River Basin each year and monitored with dozens of remote detection systems located at constriction points in migration, such as dam bypasses (see the PIT Tag Information System [PTAGIS]; www.ptagis.org).

Tag return data from commercial fisheries can also be enhanced by using PIT tags and remote detection systems placed at bottlenecks during harvest and processing. By placing remote detection systems on selected vessels and combining PIT tags with conventional T-bar tags, researchers were able to precisely estimate tag reporting rates, exploitation rates, and natural mortality for southern rock lobsters (*Jasus edwardsii*) in Australia (Burch et al. 2009; Frusher et al. 2009). For fisheries with larger bottlenecks at processing facilities, antennas or arrays of antennas could be incorporated into the processing line. For example, antennas could be constructed to fit the brailers at processing facilities for Bristol Bay-Bering Sea crab fisheries to detect tagged crabs as they are offloaded from the boats. Bottlenecks in processing occur in many other fisheries, such as whitefish stocks in the Great Lakes and shrimp stocks in the Gulf of Mexico and the Pacific Ocean, and we suspect that remote detection systems could be integrated into these facilities. The benefits to inference and estimation should be worth the initial costs and public relations work that would be required.

Finally, encounter data from remote detection systems can benefit analyses that integrate multiple sources of information through a joint likelihood approach. For example, tag returns from fishermen can be combined with telemetry studies (Pollock et al. 2004) as well as various sources of fishery-dependent data (Coggins et al. 2006; Eveson et al. 2007, 2009; Conn et al. 2009). An integrated model that incorporates information from tag re-encounters can often disentangle parameters of interest that are otherwise not estimable, such as tag reporting rate. The future of assessments for large commercial fisheries appears to lie in such integrated modeling (Maunder 2003), but other population dynamics investigations can benefit from such an approach as well. Remote detection systems for PIT tags offer potential for dramatically increasing encounter probabilities and the density of data provided by tagged individuals, which would benefit a wide range of fisheries studies.

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