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Sensitivity of tag-recovery mortality estimates to inaccuracies in tag shedding, handling mortality, and tag reporting

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ABSTRACT

We used Monte Carlo simulations to evaluate the sensitivity of tag-recovery mortality estimates to inaccuracies in tag shedding, handling mortality, and tag reporting. The data-generating model used in the simulations assumed that tagging was conducted annually for 4 years with tag recoveries occurring over a 4-year period. Several different combinations of instantaneous fishing (F) and natural (M) mortality were evaluated in the simulations. The data-generating model additionally assumed that immediate-shedding and handling-mortality rates equaled 2.5% and 0%, respectively, and that chronic shedding was a sigmoidal function of months since tagging. Two spatial patterns of reporting rates were considered—one where reporting was a function of distance from the tagging site and one where reporting was a random generation across the study area. Maximum likelihood estimates of F and M were calculated from the recovery of tags from the data-generating model under different assumed rates of tag shedding, handling mortality, and tag reporting. We found that assumptions about reporting rates resulted in the most variability in mortality estimates regardless of which combination of F and M was evaluated, with assumptions about chronic shedding also contributing substantially to overall variability in mortality estimates for most mortality combinations. Assumptions about immediate tag shedding and handling mortality had relatively minor effects on mortality estimates compared to reporting rate. When planning a tag-recovery study, care should be taken to ensure that chronic shedding and tag-reporting rates are accurately measured, as inaccurate measurements in these factors can result in significant errors in mortality estimates.

Introduction

Tag-recovery models (Brownie et al., 1985) are widely used to estimate mortality of both marine and freshwater fish stocks. Several factors, including tag shedding, handling mortality, and tag reporting, can affect the numbers of recovered tags and, as a consequence, mortality estimates. While it is possible to estimate at least some of these rates when fitting a tag-recovery model, accurate estimation can be difficult (Hoenig et al., 1998; Denson et al., 2002). As a result, accurate mortality estimation using a tag-recovery approach at least partly depends on the collection of auxiliary data pertaining to tag shedding (hereafter referred to as shedding), handling mortality, and tag reporting (hereafter referred to as reporting). Each of these factors can be measured in a variety of ways: shedding can be estimated by double tagging or supplemental marking of fish (Pierce and Tomcko, 1993; Fabrizio et al., 1999; Latour et al., 2001; Miranda et al., 2002, Livings et al., 2007); handling mortality can be estimated by withholding samples of tagged fish in tanks, pens, or cages (Pierce and Tomcko, 1993; Latour et al., 2001; Miranda et al., 2002; Taylor et al., 2006); reporting rates can be estimated through the use of high-reward tags (Pollock et al., 2001; Pollock et al., 2002; Taylor et al., 2006), planted tags (Hearn et al., 2003), or creel or port surveys (Hearn et al., 1999; Pollock et al., 2002).

Even when data concerning shedding, handling-mortality, and reporting rates are collected as part of a tagging study, biased mortality estimates may still result if measurements of these rates are not accurate (Miranda et al., 2002). For example, handling mortality may be overestimated if fish held in nets or pens become stressed as a result of biofouling (Ahlgren, 1998; Udomkusonsri and Noga, 2005; Isermann and Carlson, 2008). Alternatively, handling mortality may be underestimated if favorable conditions in tanks promote the recovery of tagged specimens. In either case, biased mortality estimates would result because of the inaccuracies in handling-mortality data. Knowing how such inaccuracies can influence mortality estimates can be beneficial when planning a tagging study as more resources can be devoted to measuring those factors that can result in the largest biases in the estimates.

Our interest in how inaccuracies in shedding, handling-mortality, and reporting rates can affect estimation of fishing and natural mortality stemmed from our involvement in a project meant to clarify the

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relationship between indicators of fish health and natural mortality rates in four lake whitefish (*Coregonus clupeaformis* Mitchill) stocks in northern lakes Huron and Michigan (Wagner et al., 2010). For that study, lake whitefish were tagged with anchor tags, and the recovery and reporting of tags by commercial fishers was used to estimate fishing and natural mortality rates for the stocks (Ebener et al., 2010a). Data pertaining to shedding, handling mortality, and reporting were collected as part of the study; however, there was concern that measurements of some of these factors were inaccurate. For example, one way that handling mortality was monitored was by holding a subsample of tagged fish at an onshore facility. While at this facility, though, many tagged fish developed fungal infections and died. The cause of these infections was believed to be the transport and holding of fish at the onshore facility rather than the tagging process. As a result, we did not use this information when calculating handling-mortality rates. Even though we ultimately did not to use this information, it still caused us to question whether our estimates of handling mortality were accurate, and, if not, how our estimates of fishing and natural mortality might be affected by the inaccuracy.

Another factor that concerned us with the lake whitefish study was how possible spatial differences in reporting rates might affect mortality estimation. For the lake whitefish study, reporting rates by commercial fishermen were measured through onboard observers. Reporting rates were not calculated as part of the tag-recovery model; rather, reporting rates for the stocks were calculated separately and were used as constants when specifying the tag recovery probabilities for the estimation model (e.g., Latour et al., 2001). Given the sizes of the systems that we were studying, we believed it was possible, if not likely, that reporting rates varied depending on where tags were recovered from the lakes regardless of whether exploitation was constant across the study area or not. Reporting rates are likely affected by many factors, such as publicity of the tagging program, prior acquaintanceship between fishers and study investigators, perceptions of fishers as to how the tagging information will be used, and general fisher indifference to the tagging program. It is widely recognized that changes in factors such as these can lead to reporting rates that vary with time (Pollock et al., 2002; Polacheck et al., 2006; Taylor et al., 2006). However, spatial differences in tag reporting rates also are likely to occur (Jenkins et al., 2000; Denson et al., 2002), which may be a significant source of error when estimating mortality.

The purpose of this research was to evaluate the sensitivity of tag-recovery mortality estimates to inaccuracies in shedding, handling-mortality, and reporting rates. This analysis should provide useful information regarding the sensitivity of mortality estimates to possible inaccuracies of these factors, and thereby guide planning of tagging studies to ensure that mortality estimates are as accurate as possible.

Methods

We used Monte Carlo simulations to explore the sensitivity of tag-recovery mortality estimates to errors in assumed rates of shedding, handling mortality and reporting. Our simulations consisted of a data-generating model that generated tag recoveries, and an estimation model that used the number of recovered and reported tags to estimate instantaneous fishing and natural mortality rates. We based our simulations on the tagging protocol and spatial framework of the aforementioned lake whitefish study. For our data-generating model, tagged fish were released annually for 4 years, with tag recoveries occurring over a 4-year period that began with the initial tagging event. Fish were assumed to be tagged at a single site in northern Lake Michigan, with recovery of tags occurring at locations throughout the lake (Fig. 1). A target tagging level of 2,000 fish per year was used for the data-generating model, although the actual number of tagged fish in a year was determined by random draw from a normal distribution with a mean equal to the target tagging effort and a standard deviation equal to 5% of the mean. The resulting value was then rounded to the nearest integer. Immediately after tagging, fish dispersed to various parts of the lake, with dispersal being a function of distance from the tagging site. The fraction of tagged fish dispersing to areas within 25 km, from 25 to 50 km, from 50 to 100 km, from 100 to 200 km, and beyond 200 km of the tagging site was a random draw from a multinomial distribution with expected cell probabilities of 70%, 15%, 10%, 4%, and 1%, respectively, which was similar to the observed dispersal of lake whitefish from the tagging study (Ebener et al., 2010b). Dispersal of fish to individual 10-min grids within these distances of the tagging site was random. After dispersal, it was assumed that fish remained within their occupied grid cells throughout the duration of the study, which we assumed primarily for the sake of simplicity. Conceptually, the tagging site represented a spawning area for the lake whitefish population, while the dispersal locations represented feeding areas occupied by the lake whitefish during other times of the year.

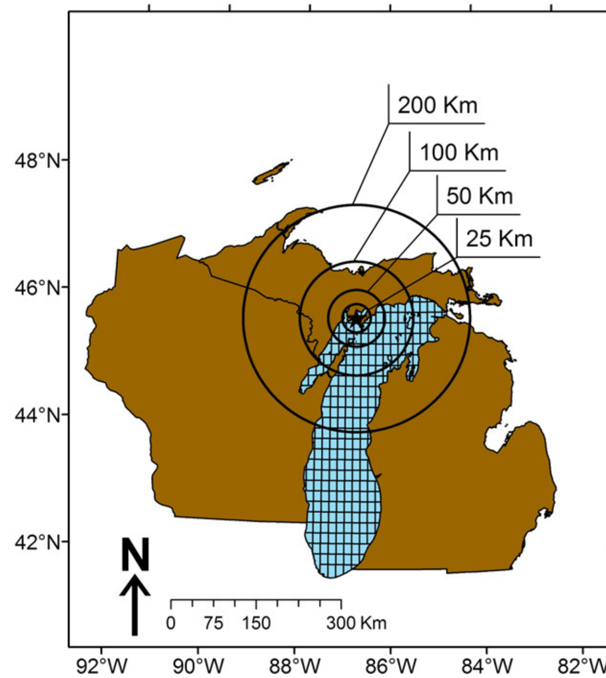

Fig. 1. The assumed spatial framework used in our simulations to evaluate the sensitivity of tag-recovery mortality estimates to shedding, handling mortality, and reporting rate inaccuracies. Fish were assumed to be tagged at a single site in northern Lake Michigan (&), whereupon fish dispersed to various Lake Michigan 10-min grids. The concentric circles around the tagging site indicate various distances from the tagging site.

Recovery of tags for the data-generating model were determined using the Hoenig et al. (1998) instantaneous mortality formulation of a tag-recovery model for an assumed Type-II (continuous fishing throughout the year) fishery. Several different combinations of instantaneous fishing (F) and natural mortality (M) were incorporated in the data-generating model and evaluated in our simulations: high F and high M ($F=0.40$ and $M=0.40$), high F and low M ($F=0.40$ and $M=0.15$), low F and high M ($F=0.15$ and $M=0.40$), and low F and low M ($F=0.15$ and $M=0.15$). To mimic our lake whitefish study, we divided the year into three seasons that differed in both length of year and amount of harvest. The fraction of the year for the seasons was 0.417 (season 1), 0.333 (season 2), and 0.25 (season 3). The fraction of the harvest for the seasons was 0.19 (season 1), 0.40 (season 2), and 0.41 (season 3). For simplicity, we assumed that fishing and natural mortality were constant throughout the lake and for each year of the study. We also assumed that the fraction of the harvest that occurred in each season was constant.

We assumed a handling-mortality rate of 0% and an immediate-shedding rate of 2.5% for the data-generating model. Chronic shedding was assumed to be a sigmoidal function of months since tagging and was calculated with the equation

$$\gamma_t = \frac{\alpha}{1+\exp(\beta - t)} = \frac{0.31}{1+exp(8.5-t)}, \tag{1}$$

where γ_t was the chronic-shedding rate by month, t was the number of months since tagging, and α and β were model parameters describing the maximum shedding rate and the function inflection point, respectively. With this function, chronic shedding was near zero for the first 5 months after tagging, and then progressively increased during the next several months before stabilizing at a shedding rate of 31% at 12 months post-tagging. This pattern in chronic shedding, as well as the rates associated with handling mortality and immediate shedding, corresponded to our observations in the lake whitefish study (see Ebener et al., 2010a), and are similar to rates that have been reported in the literature (Ebener and Copes, 1982; Muoneke, 1992; Pierce and Tomcko, 1993; Fabrizio et al., 1996; Hearn et al., 1999; Buzby and Deegan, 1999; Pollock et al., 2001; Miranda et al., 2002; Polacheck et al., 2006; and Taylor et al., 2006).

We considered two spatial patterns of reporting rates in our data-generating model. In the first instance, reporting rate was a function of distance from the tagging site and was calculated with the equation

$$RR_i = 0.5 \cdot exp(-0.015 \cdot y_i) + 0.25, \tag{2}$$

where RR_i was the reporting rate for grid i and y_i was the distance in kilometers of the centroid of grid i from the tagging site. This equation resulted in reporting rates that ranged from 25% to 60% for the study area (Fig. 2). In the second instance, reporting rates for Lake Michigan grids were generated randomly from a uniform distribution with lower and upper bounds equal to 25% and 60%, respectively (Fig. 2). These simulated reporting rates again reflected our observations for the lake whitefish study (Ebener et al., 2010a), and are similar to reporting rates that have been published elsewhere (Jenkins et al., 2000; Polacheck et al., 2006).

Like the data-generating model, our estimation model for the simulations was based on the Hoenig et al. (1998) instantaneous mortality formulation of a tag-recovery model for an assumed Type-II fishery. With the estimation model, however, F and M were model unknowns that were estimated based on the number of recovered tags from the data-generating model. With the estimation model, we assumed several different rates and functions for shedding, handling mortality, and reporting so that sensitivity of mortality rate estimates to inaccuracies in these factors could be evaluated. For handling mortality and immediate shedding, we evaluated rates of 0.0%, 2.5%, 5.0%, and 10.0% (actual values in the data-generating model were 0% for handling mortality and 2.5% for immediate shedding). For chronic shedding, we considered four functions that related chronic shedding of tags to months since tagging (Fig. 3). Function 1 (CS1) was the same equation used in the data-generating model, and thus represented the case where chronic shedding was accurately measured. Functions 2 (CS2) and 3 (CS3) were similar to CS1, but had different values for the inflection point (β). For CS2, β equaled 12, while for CS3 β equaled 5. Thus, CS2 corresponded to a situation where the largest change in tag shedding was believed to occur later than it actually occurred, while CS3 corresponded to a situation where it was believed to occur earlier than actual (Fig. 3). For Function 4 (CS4), chronic shedding was assumed to be asymptotically related to the number of months since tagging, with the probability of tag loss rapidly increased during the first few months after tagging before stabilizing at 31% approximately 12 months after tagging (Fig. 3).

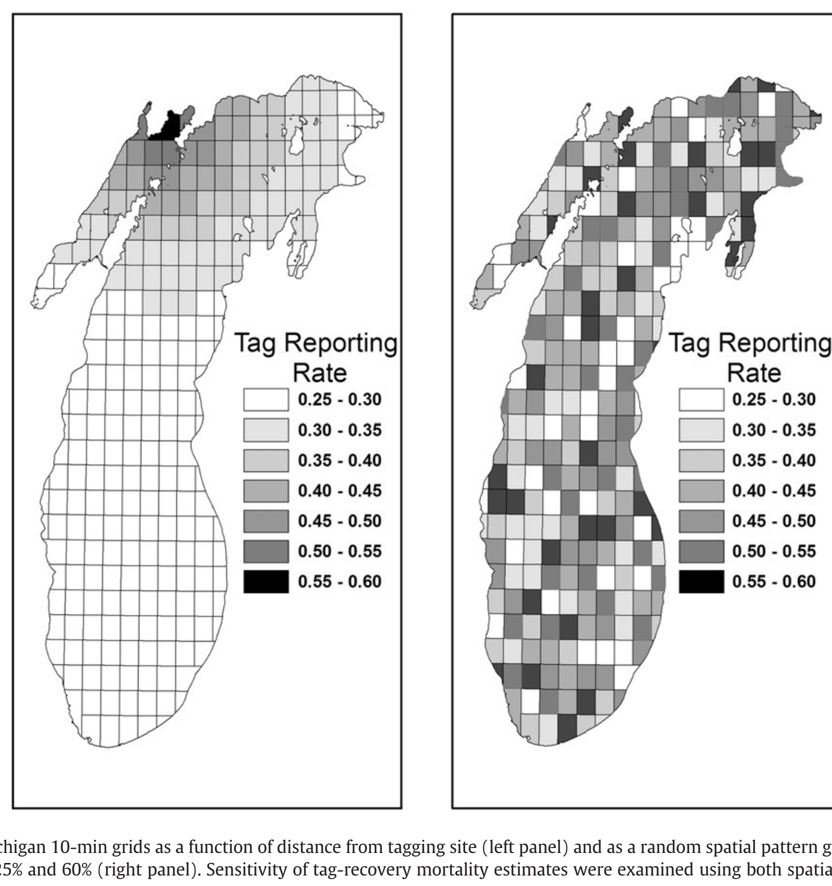

Fig. 2. Reporting rates for Lake Michigan 10-min grids as a function of distance from tagging site (left panel) and as a random spatial pattern generated from a uniform distribution with lower and upper bounds of 25% and 60% (right panel). Sensitivity of tag-recovery mortality estimates were examined using both spatial reporting rate patterns in the data-generating model.

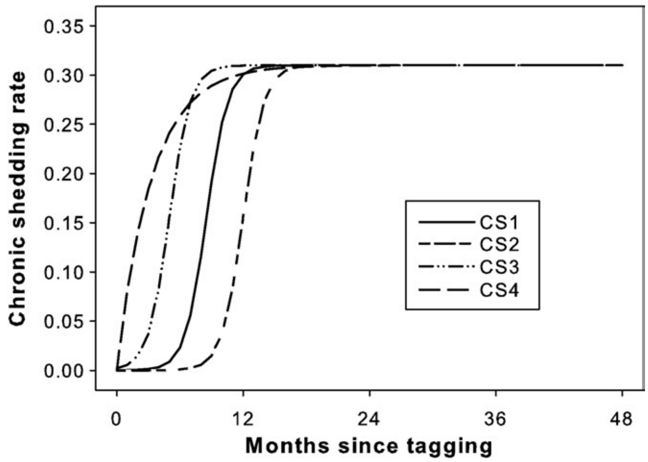

Fig. 3. Chronic-shedding functions that were evaluated in the estimation model. See manuscript text for a description and parameterization of each function.

For reporting, we considered scenarios where reporting rates were believed to equal 25%, 40%, or 60%. These rates were equivalent to the minimum, mid-range, and maximum reporting rates that were used in the data-generating model.

We used the macro capabilities of SAS Version 9.1 (SAS Institute, Inc., 2003) to conduct our simulations. One hundred simulations were conducted for each *F* and *M* combination and spatial reporting rate pattern used in the data-generating model and assumed rates and functions for shedding, reporting, and handling mortality in the estimation model. Maximum likelihood estimates of *F* and *M* for the data-estimation model were obtained using the NLP procedure (SAS Institute, Inc., 2007). Annual estimates of *F* and a constant estimate of *M* were obtained for each simulation run. The objective function for the estimation model, which consisted of the summed multinomial negative log-likelihoods for the four tagged cohorts in the simulations, was minimized using quasi-Newton optimization (SAS Institute, Inc., 2007).

The prediction errors under different levels of shedding, handling-mortality, and reporting rate inaccuracies were evaluated by calculating the relative error and absolute relative error of the estimates of *F* and *M*. Systematic over- or under-estimation of mortality rates was evaluated based on the mean of the relative errors. Relative performance of the estimation model under different assumed rates and functions of reporting, shedding, and handling mortality was compared based on the differences in the mean of the absolute relative errors of the mortality estimates. Additionally, we used variance components analysis to determine how much of the observed variability in the mortality estimates was contributed by our assumptions concerning shedding, handling mortality, and reporting. The variance components analysis was conducted using a random-effects model to relate *F* and *M* to the different shedding, handling-mortality, and reporting rates and functions considered in this study. The random-effects models were fit in SAS using the MIXED procedure (SAS Institute, Inc., 2004).

Results

Altogether, we explored 1,536 variable combinations in our simulations (4 *F* and *M* combinations × 2 spatial reporting rate patterns × 3 assumed reporting rates × 4 assumed chronic-shedding functions × 4 assumed immediate-shedding rates × 4 assumed handling-mortality rates). There was substantial overlap in estimates of *F* and *M* between the different reporting rate patterns for the various mortality combinations that were included in the data-generating model (Table 1). Mean estimates of *F* from the simulations were generally greater when reporting rate was a function of distance from the tagging site, but estimates of *M* were lower. Although the ranges of mortality estimates were generally wider when reporting rate was a random spatial pattern, the coefficient of variation for the mortality estimates were sometimes larger when reporting rate was a function of distance from the tagging site (Table 1). The coefficient of variation was larger for estimates of *M* than for estimates of *F*, and was generally larger when the combination of mortality rates in the data-generating model included a low *M*.

Overall, we found that sensitivity of mortality estimates to different assumed rates and functions of shedding, handling mortality, and reporting were similar for the various combinations of *F* and *M* included in the data-generating model. There were of course some

Table 1
Mean, minimum (Min.), maximum (Max.), and coefficient of variation (CV) of instantaneous fishing and natural mortality estimates for the different combinations of *F* and *M* incorporated in the data-generating model.

Data-generating mortality combination	Estimate	Distance				Random			
		Mean	Min.	Max.	CV	Mean	Min.	Max.	CV
High *F* and high *M* ($F=0.40$ and $M=0.40$)	F_1	0.58	0.27	0.96	34.15	0.52	0.19	0.95	36.65
	F_2	0.58	0.28	0.97	34.05	0.52	0.21	0.97	35.90
	F_3	0.59	0.28	1.07	35.27	0.52	0.20	1.08	36.47
	F_4	0.60	0.27	1.39	38.20	0.53	0.17	1.39	39.35
	M	0.26	<0.01	0.54	70.60	0.32	<0.01	0.72	57.95
High *F* and low *M* ($F=0.40$ and $M=0.15$)	F_1	0.53	0.27	0.74	25.76	0.49	0.19	0.74	29.74
	F_2	0.54	0.28	0.78	37.84	0.50	0.20	0.78	31.40
	F_3	0.59	0.28	0.97	34.74	0.53	0.19	0.97	37.24
	F_4	0.70	0.27	1.62	51.50	0.60	0.17	1.60	50.38
	M	0.08	<0.01	0.29	111.12	0.12	<0.01	0.46	97.32
Low *F* and high *M* ($F=0.15$ and $M=0.40$)	F_1	0.22	0.10	0.45	37.58	0.20	0.07	0.44	39.07
	F_2	0.22	0.10	0.44	36.85	0.20	0.08	0.42	37.88
	F_3	0.22	0.10	0.45	36.95	0.20	0.07	0.45	38.47
	F_4	0.22	0.10	0.47	37.20	0.20	0.07	0.51	40.05
	M	0.36	0.17	0.53	23.20	0.38	0.11	0.68	23.82
Low *F* and low *M* ($F=0.15$ and $M=0.15$)	F_1	0.22	0.10	0.43	37.38	0.20	0.07	0.43	38.76
	F_2	0.22	0.10	0.43	36.87	0.20	0.07	0.44	37.79
	F_3	0.22	0.10	0.45	37.37	0.20	0.07	0.47	38.56
	F_4	0.23	0.10	0.48	38.05	0.20	0.07	0.52	40.33
	M	0.11	<0.01	0.27	72.69	0.13	<0.01	0.42	65.26

Annual estimates of *F* ($F_1 - F_4$) and a constant estimate of *M* were obtained from the estimation model. Simulations were conducted using two spatial patterns in reporting rates for the data generating model; one where reporting was a function of distance from the tagging site (Distance) and the other where reporting was randomly generated (Random). See Fig. 2 for a representation of these spatial reporting rate patterns. Summary statistics are calculated over the ranges of assumed rates and functions for reporting, shedding, and handling mortality.

differences in the relative error and absolute relative error values as well as the variance estimates from the variance components analyses of the mortality estimates, but the salient results as to what factors caused the largest errors in mortality estimates were similar. Thus, for the sake of brevity, we focus on the results of the low *F* and high *M* mortality combination, which was the mortality combination that we believed at the outset of out lake whitefish study was closest to actual mortality rates. We do, however, note where appropriate results that differed for particular combinations of *F* and *M* in the data-generating model.

From a general standpoint, the most accurate estimates of mortality were obtained with an assumed reporting rate of 60% when reporting in the data-generating model was a function of distance from the tagging site. With this assumed rate of reporting, mean relative errors were closest to zero regardless of what the assumed rates and functions were for shedding and mortality (Fig. 4). When reporting in the data-generating model was a random spatial pattern, assumed reporting rates of 40% and 60% performed about equally well with a 60% reporting rate generally overestimating *F* and underestimating *M* and a 40% reporting rate underestimating *F* and overestimating *M* (Fig. 5). It should be noted however that mean relative errors near zero were obtainable at several different combinations of reporting, handling-mortality, and shedding rates and functions, which illustrates the confounding of mortality estimates to these factors. For example, when reporting rates were a function of distance from the tagging site, mean relative errors near zero for *F* were obtained with an assumed reporting rate of 60%, the CS4 chronic shedding function, and handling-mortality and immediate-shedding rates of 0% (Fig. 4). Mean relative errors near zero for *F* and *M* were also obtained with an assumed reporting rate of 40%, the CS2 chronic shedding function, and immediate-shedding and handling-mortality rates of 0% (Fig. 4). With a random spatial reporting rate in the data generating model, there were larger ranges in relative errors of mortality estimates than when reporting was a function of distance from the tagging site (Figs. 4 and 5).

We found that assumptions about reporting had the largest effect on errors in mortality rates for both spatial reporting rate patterns. When reporting rates for the study area were a function of distance

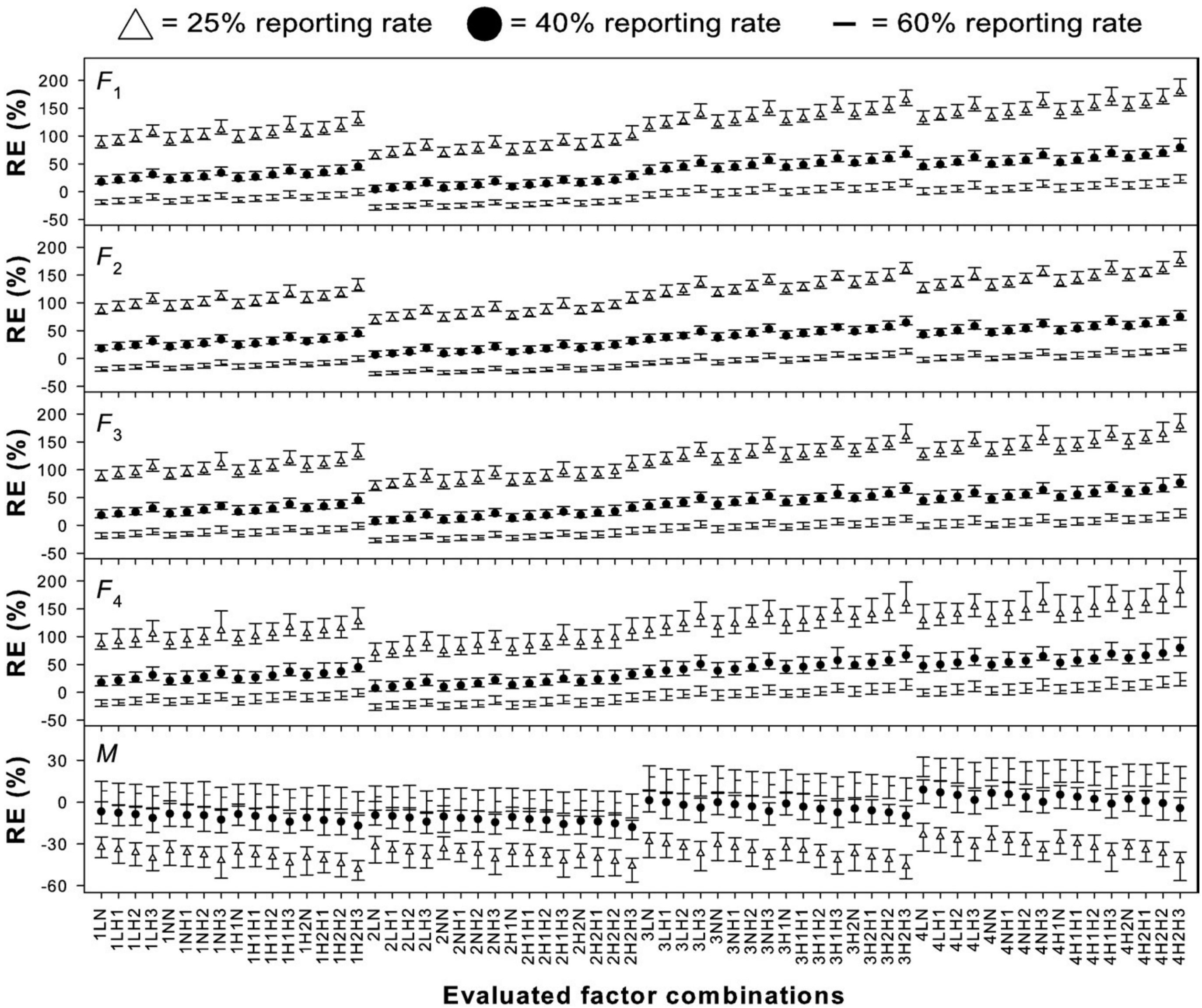

Fig. 4. Mean relative error of the annual estimates of fishing mortality (Year 1 = F_1, Year 2 = F_2, Year 3 = F_3, Year 4 = F_4) and natural mortality (*M*) for the chronic shedding, immediate shedding, and handling mortality combinations when reporting in the data-generating model was a function of distance from the tagging site. Error bars denote the minimum and maximum relative errors observed in the simulations for that combination of factors. The *x*-axis identifies the particular combination of chronic-shedding functions (CS1 = 1, CS2 = 2, CS3 = 3, CS4 = 4), immediate-shedding (L = 0%, N = 2.5%, H1 = 5%, H2 = 10%), and handling-mortality rates (N = 0%, H1 = 2.5%, H2 = 5%, H3 = 10%) for which the errors correspond (example: 2LH1 = CS2, 0% immediate shedding, and 2.5% handling mortality).

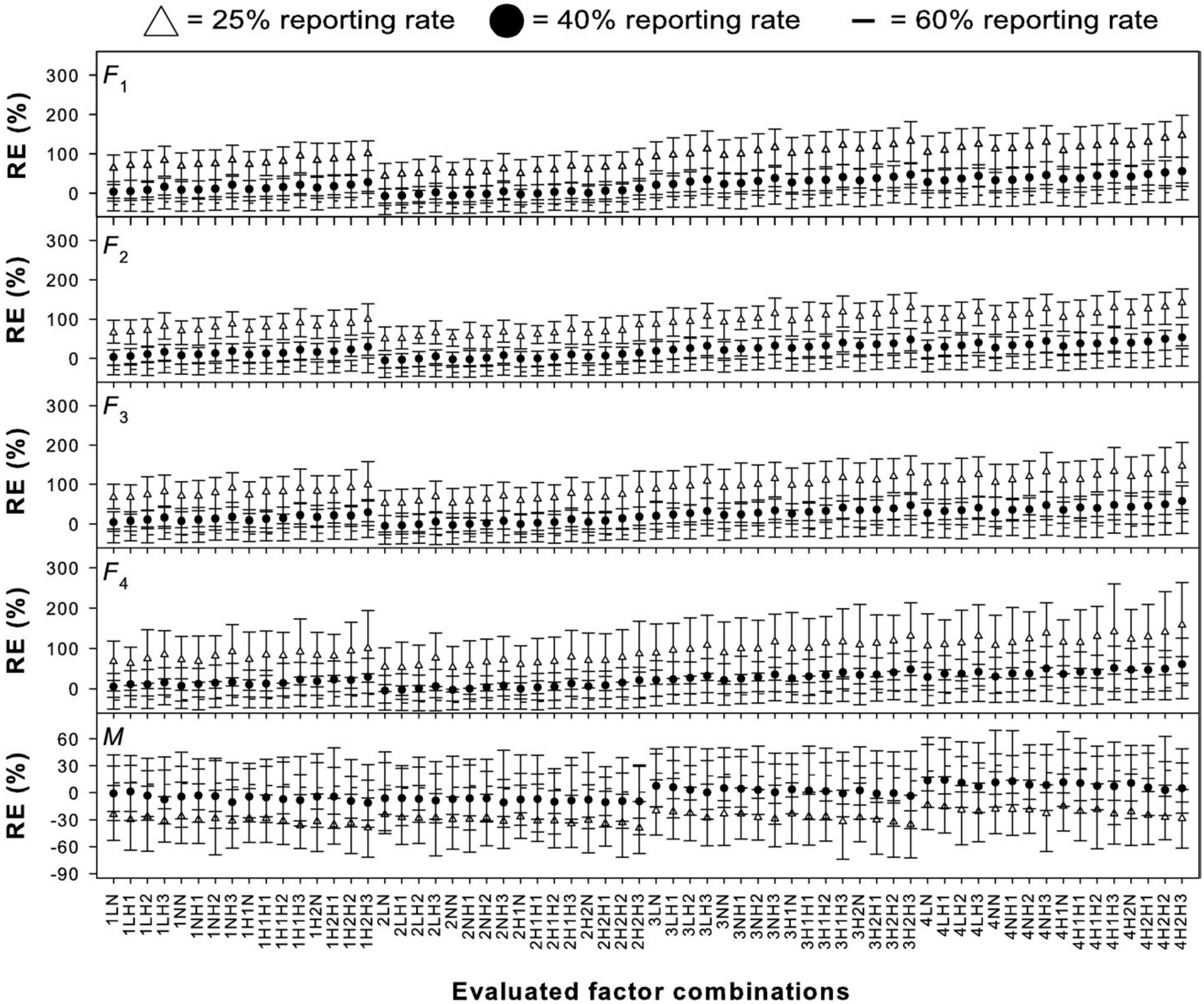

Fig. 5. Mean relative error of the annual estimates of fishing mortality (Year 1 = F_1, Year 2 = F_2, Year 3 = F_3, Year 4 = F_4) and natural mortality (M) for assumed rates and functions of reporting, chronic shedding, immediate shedding, and handling mortality when reporting in the data-generating model was a random spatial pattern generated from a uniform distribution. Error bars denote the minimum and maximum relative errors observed in the simulations for that combination of factors. The *x*-axis identifies the combination of chronic-shedding functions (CS1 = 1, CS2 = 2, CS3 = 3, CS4 = 4), immediate-shedding (L = 0%, N = 2.5%, H1 = 5%, H2 = 10%), and handling-mortality rates (N = 0%, H1 = 2.5%, H2 = 5%, H3 = 10%) for the corresponding errors (example: 2LH1 = CS2, 0% immediate shedding, and 2.5% handling mortality).

from the tagging site, mean absolute relative errors in *F* for an assumed reporting rate of 25% were between 60% and 103% larger, depending on assumed shedding and handling-mortality rates and functions, than mean relative errors for an assumed reporting rate of 40%, while mean absolute relative errors in *M* were between 15% and 37% larger. When compared to a 60% assumed reporting rate, mean absolute relative errors for an assumed reporting rate of 25% were between 33% and 162% larger for estimates of *F* and anywhere from 2% lower to 46% larger for estimates of *M*. Compared to a 60% assumed reporting rate, mean absolute relative errors for an assumed reporting rate of 40% were between 26% lower and 59% larger for estimates of *F* and anywhere from 19% lower to 15% larger for estimates of *M* depending on the other assumed rates and functions for shedding and handling mortality.

When the data generating model used the random spatial pattern for reporting, mean absolute relative errors in *F* for an assumed reporting rate of 25% were between 35% and 92% larger, depending on assumed shedding and handling-mortality rates and functions, than mean absolute relative errors for an assumed reporting rate of 40%, while mean absolute relative errors in *M* ranged from nearly equal to 26% larger. When compared to a 60% assumed reporting, mean absolute relative errors for an assumed reporting rate of 25% were between 5% and 145% larger for estimates of *F* and anywhere from 12% lower to 29% larger for estimates of *M*. Compared to a 60% assumed reporting rate, mean absolute relative errors for an assumed reporting rate of 40% were anywhere from 30% lower to 48% larger for estimates of *F* and from 16% lower to 5% larger for estimates of *M*.

Differences in the mean absolute relative errors for the different chronic shedding functions depended on which functions were compared, but differences were typically smaller than they were for the assumed reporting rate comparisons. This was the case when reporting rates in the data-generating model were a function of distance from the tagging site and when they were a random spatial pattern. The largest differences in mean absolute relative errors for the chronic shedding functions were between CS2 and CS4 functions. Mean absolute relative errors in *F* for the CS2 function differed anywhere from 25% larger to 80% smaller when compared to the CS4 function depending on the other assumed rates for shedding, handling mortality, and reporting. Mean absolute relative errors in M for the CS2 function differed anywhere from 21% lower to 9% larger when compared to the CS4 function. The CS2 and CS4 shedding functions differed the most of all the functions as to when most tags were shed. With the CS2 function, it was assumed that most tags were initially retained for several months before most shedding occurred, while for CS4 it was assumed that most tags were shed relatively shortly after tagging (Fig. 3). When comparing other functions (e.g., CS1 versus CS2, CS1 versus CS3), the differences in mean absolute relative errors for the mortality estimates were substantially smaller, often on the order of a 20% difference for the two functions.

For both immediate shedding and handling mortality, the differences in mean absolute relative errors between the different assumed rates when other factors were held constant were small regardless of the underlying reporting pattern for the data-generating model. Mean absolute relative errors for estimates of F differed by less than 20% when they were compared across the different assumed rates for immediate shedding and handling mortality. For M, mean absolute relative errors generally differed by less than 10% when they were compared across the different assumed rates for immediate shedding and handling mortality.

The results from the variance components analysis of the simulation mortality estimates confirmed that assumptions about reporting explained the most variability in estimates of mortality estimates. This was the case regardless of whether reporting rates in the data-generating model were a function of distance from the tagging site or were a random spatial pattern. When reporting rate was a function of distance from the tagging site, the variance estimates for the reporting-rate effect was between 55 and 81 times larger than the residual variance for annual estimates of F, and 34 times larger than the residual variance for M (Fig. 6). When reporting rate in the data-generating model was a random spatial pattern, the variance estimates for the reporting-rate effect was between 7 and 21 times larger than the residual variance estimates for annual estimates of F and was 2.5 times larger than the residual variance estimate for M (Fig. 7). The differences in variance ratios between the two reporting-rate patterns assumed in the data-generating model were due largely to an increase in the residual variance estimate for the random spatial pattern, as the variance estimates for the other random effects were similar in value between the reporting-rate patterns (Figs. 6 and 7).

Chronic shedding explained the next largest fraction of the observed variability in annual estimates of F. The variance estimates for the chronic-shedding functions were between 6 and 8 times larger than the residual variance estimated when reporting rates were a function distance from the tagging site (Fig. 6), and were between one and two times larger than the residual variance with the random spatial pattern of reporting (Fig. 7). Chronic shedding also generally explained the next largest fraction of the observed variability in M; however, the ratio of the variance estimate for chronic shedding in relation to the residual variance estimate differed for the two reporting-rate patterns. When reporting rate for the data-generating model was a function of distance from the tagging site, the variance estimate for chronic shedding was three times larger than the residual variance. When reporting rates in the data-generating model were a random spatial pattern, the variance estimate for chronic shedding was approximately one-third that of the residual variance. The one notable exception to chronic shedding explaining the second largest fraction of the observed variability in M was when the high F and low M mortality combination was incorporated in the data generating model. With this mortality combination, chronic shedding explained the smallest fraction of observed variability in M and had variance estimates that were roughly five-times smaller than those for immediate shedding and handling mortality. This may have in part been due to the mortality estimate hitting a lower bound during the estimation process for certain assumed rates and functions of shedding, handling mortality, and reporting.

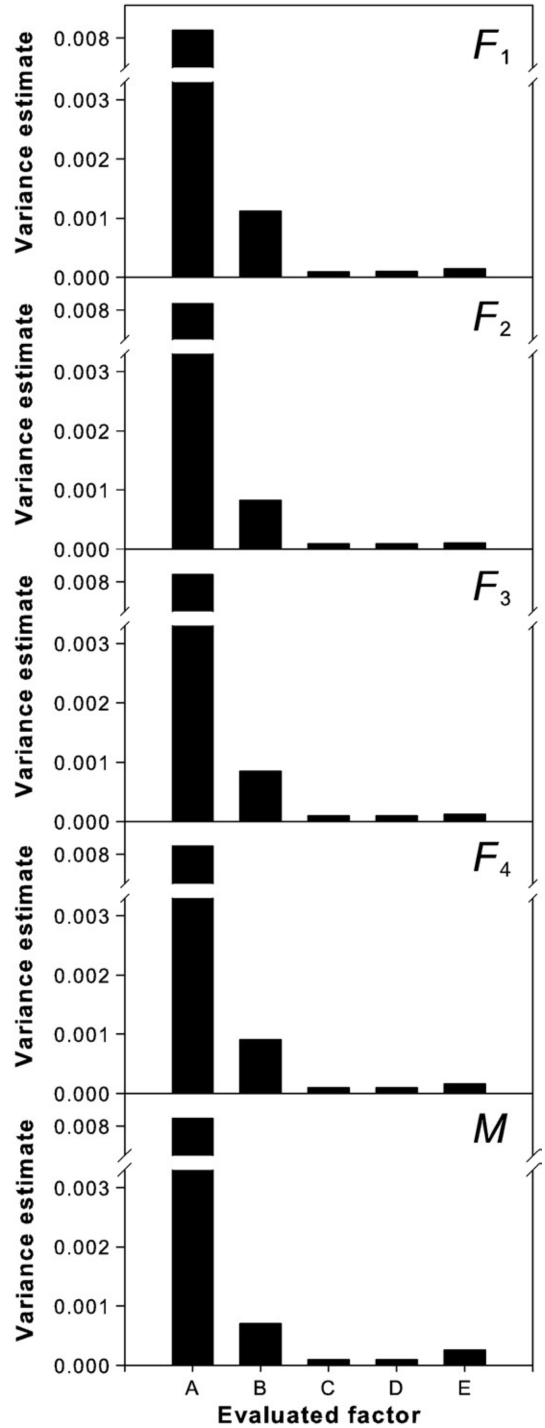

Fig. 6. Estimated variance components for the annual estimates of fishing mortality (Year 1 = F_1, Year 2 = F_2, Year 3 = F_3, Year 4 = F_4) and natural mortality (M) based on a random-effects model with assumed rates and function of reporting, chronic shedding, immediate shedding, and handling mortality as independent variables when reporting in the data-generating model was a function of distance from the tagging site: A = Reporting; B = Chronic shedding; C = Immediate shedding; D = Handling mortality; E = Residual variance).

The amount of observed variability in the mortality estimates explained by handling-mortality and immediate-shedding rates was low for both reporting rate patterns used in the data-generating model. When reporting rates in the data-generating model were a function of distance from the tagging site, the variance estimates for handling mortality and immediate shedding were between 0.6 and 0.9 times that of the residual variances for annual estimates of F, and

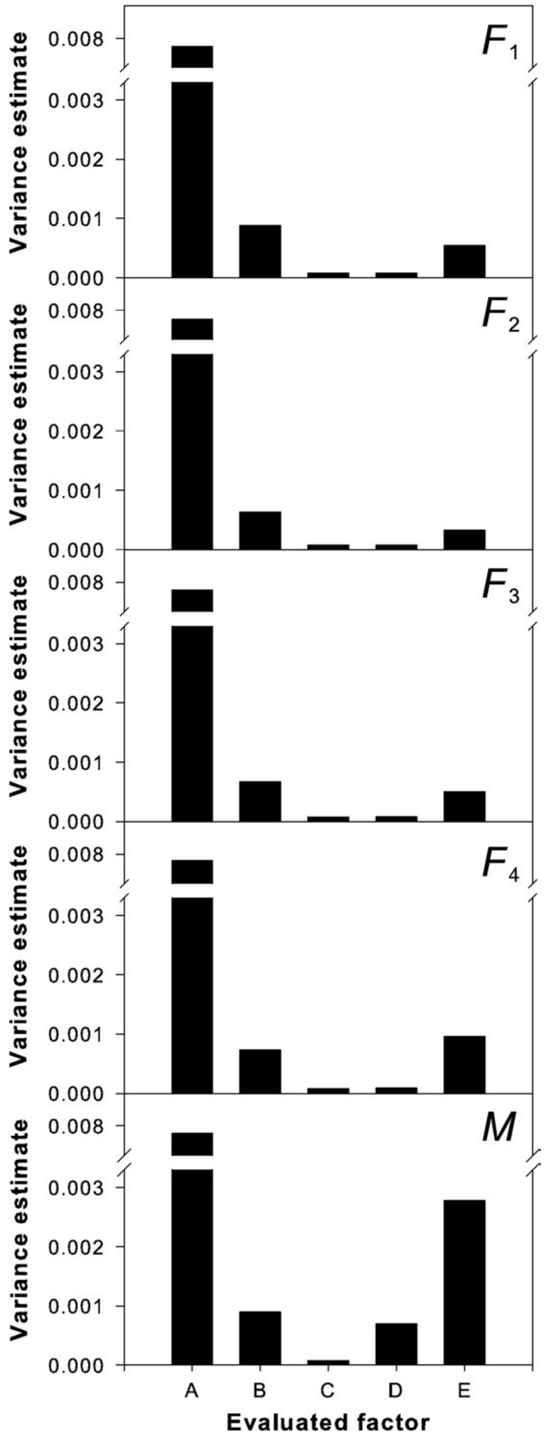

Fig. 7. Estimated variance components for the annual estimates of fishing mortality (Year 1 = F_1, Year 2 = F_2, Year 3 = F_3, Year 4 = F_4) and natural mortality (M) based on a random-effects model with assumed rates and function of reporting, chronic shedding, immediate shedding, and handling mortality as independent variables when reporting in the data-generating model was a random spatial pattern generated from a uniform distribution: A = Reporting; B = Chronic shedding; C = Immediate shedding; D = Handling mortality; E = Residual variance).

was 0.4 times that of the residual variance for M (Fig. 6). When reporting rates in the data-generating model were a random spatial pattern, the variance estimates for handling mortality and immediate shedding were between 0.1 and 0.2 times that of the residual variances for annual estimates of F, and was less than 0.03 times that of the residual variance for M (Fig. 7).

Discussion

When planning a tagging study, a number of decisions must be made, such as how many fish will be tagged, how much of a reward will be offered for the return of tags, and how much effort will be devoted to collecting information regarding shedding, handling mortality, and reporting (Guy et al., 1996). Because of budget constraints, the answer to one of these questions will affect the answers to other questions. The reward offered for tag returns will depend on how many fish are tagged and expected return rates. The employment of observers to measure reporting may limit how many tags initially can be purchased. When planning a tagging study, one strives to optimally allocate resources so that mortality estimates are as accurate and precise as possible. Determining the optimal allocation of resources will be challenging because of the range of conditions that one may encounter with a tagging study, and will, among other factors, be influenced by the species and fishery that the researchers are studying. The intent of our research was to evaluate the sensitivity of tag-recovery mortality estimates to inaccuracies in shedding, handling mortality, and reporting rates to provide beneficial information to those planning on conducting their own tagging study, particularly but not exclusively for whitefish fisheries.

In conducting this study, we made several assumptions concerning fish behavior and the models that were used both to generate tag recoveries and to estimate F and M. Among the most important were that tagged fish were representative of and thoroughly mixed with the population at large, the fate of each fish was independent, all fish had the same survival and capture probabilities, the fate of each fish could be modeled as a multinomial random variable, the year and season of tag recoveries was known, fish dispersal was an immediate event, after dispersal fish did not move between cells or back to the tagging site, and fishing and natural mortality rates were constant across years (Brownie et al., 1985; Pollock et al., 2001). These are all common assumptions for this type of study, even though some, such as immediate dispersal and a subsequent lack of movement after dispersal, may not seem realistic for fish populations such as the Lake Michigan lake whitefish that formed the basis for this study. The advantage of a simulation study is that we can examine the performance of the mortality estimators when these simplifying assumptions are met, which in our view is a valuable and appropriate initial step. Adding more biological complexity would have made interpretation of our findings even more challenging than it already was. Here we have shown that spatial differences in reporting rates and to a lesser extent temporal differences in shedding rates can have large affects on mortality estimates. This work could be usefully extended in a future study by relaxing some of our assumptions and determining whether the effects we have seen are robust to other aspects of fish behavior.

When planning a tagging study, careful attention should be paid to how much resources should be devoted to measuring factors that can confound mortality estimates. Based on the results of this study as well as other studies that have looked at tag reporting, we cannot overemphasize the importance of obtaining accurate information on reporting rates. Assumptions concerning reporting rates can impart significant biases on estimates of both F and M. Unfortunately, reporting rate is considered one of the most difficult variables to measure for a tagging study (Denson et al., 2002; Miranda et al., 2002), and when combined with the fact that both spatial and temporal variation in reporting rates can occur (Jenkins et al., 2000; Pollock et al., 2002; Polacheck et al., 2006; Taylor et al., 2006), should serve as a warning that significant resources may need to be devoted to measuring reporting. In retrospect it is evident that our mortality estimates (Ebener et al., 2010a) would have been improved if we had devoted more effort to measuring reporting rates, whether it had been through additional onboard observers or the simultaneous release of some high-reward tags (Pollock et al., 2001). As previously mentioned, a number of factors are likely to affect reporting by both recreational anglers and commercial fishers. Research as to why some anglers and fishers are more likely to report tags than other would be extremely beneficial to come up with solutions to increase tag reporting rates.

Accurate measurement of chronic shedding will also be beneficial when conducting tagging study. Compared to reporting rates, measurement of chronic shedding is relatively easy, and can be accomplished by either double tagging or supplementally marking tagged fish. The major question that needs to be answered is how many double-tagged or supplementally marked fish should be released. This question is particularly important for studies where tag recoveries occur over a several year period. With too few double-tagged or supplementally marked fish, shedding rates at longer time periods may only be calculated from one or two recovered individuals, which can make fitting a chronic-shedding model difficult. While a variety of models can be used to represent chronic shedding (Fabrizio et al., 1996), slight deviations in model equations may not have a strong impact on mortality estimates based on our results. Rather, it may be more important to simply capture the general trend of tag loss with time.

Despite our finding that immediate tag shedding and handling mortality had relatively minor effects on the accuracy of mortality estimates when compared to reporting, we do not recommend completely ignoring these factors when designing and conducting a tagging study. Indeed, as our study indicates, under particular mortality combinations, immediate shedding and handling mortality can have larger effects on estimates of M than immediate shedding. So while we do not suggest completely ignoring the effects of immediate shedding and handling mortality, it may not be necessary to devote substantial resources to measuring these rates, particularly if this directs resources away from obtaining accurate estimates of reporting rates.

Admittedly, the results of our study were driven by the particular rates and functions that were assumed in the data-generating and estimation models for shedding, handling mortality, and reporting. In designing our simulations, we intentionally limited our assumptions about shedding, handling mortality, and reporting to what was most likely given what was used in the data-generating model. For example, we did not consider 90% immediate shedding and handling-mortality rates in our estimation model as we felt it was highly unlikely that a measurement error of this magnitude would occur when actual immediate shedding was only 2.5%. Additionally, we attempted to incorporate rates and functions that were within the realm of acceptability based on published findings. For example, our assumption that reporting rates varied between 25% and 60% matched the range of rates that have been reported by others (Hearn et al., 1999; Pollock et al., 2001; Polacheck et al., 2006; Taylor et al., 2006). Similarly, our assumed levels of shedding was within the range reported by Ebener and Copes (1982), Muoneke (1992), Buzby and Deegan (1999), Fabrizio et al. (1996), and Miranda et al. (2002), and our assumed levels of handling mortality were similar to those reported in Pierce and Tomcko (1993) and Miranda et al. (2002). Thus, although we only considered a limited range of possibilities, we feel that the different rates and functions that were included in our simulations were appropriate and that our results accurately reflect the uncertainty associated with mortality estimation in general.

As pointed out by Pollock et al. (2001), computer simulations such as these are useful for evaluating proposed tagging study designs in light of various assumptions concerning tag reporting, handling mortality, and tag shedding. We encourage those that are considering or planning a tagging study to use simulations to help in choosing an appropriate tagging protocol. Conducting such simulations in advance will help ensure that the most accurate and precise mortality estimates are obtained given the resources available for the study.

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