FEATURE

Estimating Recycling of Fish in Catch-and-Release Fisheries

Thomas S. Jones | Minnesota Department of Natural Resources, 1200 Minnesota Avenue South, Aitkin, MN 56431. E-mail: tom.jones@state.mn.us

Matthew I. Jones | Department of Mathematics, Dartmouth College, Hanover, NH | Department of Sociology, Yale University, New Haven, CT

Melissa Treml | Minnesota Department of Natural Resources, St. Paul, MN

Thomas Heinrich | Minnesota Department of Natural Resources, Garrison, MN

Two boys fish for Smallmouth Bass Micropterus dolomieu. Photo credit: Brett Billings, U.S. Fish and Wildlife Service.

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The prevalence of catch-and-release angling for many species has increased over the past several decades. A potential benefit of catch-and-release fisheries is higher catches for anglers due to multiple captures of individual fish within a season. We term the measure of this benefit "recycling rate," defined as the total catch in a fishing season divided by the number of individuals caught at least once. Multiple-capture studies are common in the literature, but our recycling rate is a new metric that could be helpful in evaluating recreational fisheries. Estimates of recycling rate will be dependent on several factors, especially the distribution of angling selectivities among individual fish, which is generally unknown. We compared several models that estimated recycling rate based on different assumptions about angling selectivity. Application of the models to Smallmouth Bass *Micropterus dolomieu* data from Lake Mille Lacs, Minnesota, demonstrated that estimates of recycling rate were robust to assumptions about the distribution of angling selectivity.

INTRODUCTION

In his *Handbook of Freshwater Fishing* (Wulff 1939), and popularized by his famous quote, "A gamefish is too valuable to be caught only once," Lee Wulff was probably the first to propose catch-and-release angling to the public as a tool to increase angler catches. Since then, catch-and-release angling for many species in both freshwater and marine environments has become common (e.g., Muoneke and Childress 1994; Lucy and Studholme 2002). Often, catch-and-release is voluntary on the part of the anglers (Myers et al. 2008), but can also be the result of regulations (Lewin et al. 2007; Johnston et al. 2011). The motivations for catch-and-release fishing can include complex mixtures of social, economic, and conservation concerns (Arlinghaus et al. 2007). Regardless of motivation, the release and subsequent recapture of individual fish has the potential to increase within-season catches in a recreational fishery.

To quantify increases in catch resulting from multiple recaptures, we propose to define "recycling rate" as the observed total catch of all fish including recaptures divided by the number of individuals caught at least once. For example, a recycling rate of 1.5 would mean that the total catch for a season was 1.5 times what would have been expected if all fish were harvested the first time they were caught. To our knowledge, no one has presented a method for estimating recycling rates in recreational fisheries.

Other metrics have been used to assess recaptures but have not estimated recycling rate as we have defined it. Some studies counted the number of times tagged fish were reported (Bahr et al. 2018; Thorstad et al. 2019). Others have combined creel data with population estimates to report the average number of times each fish in the population was caught (Schill et al. 1986; McCormick 2016). However, neither of these metrics describes how much catch increased because of multiple recaptures. For example, if each fish is caught an average of two times, it can be difficult to distinguish between all fish being caught twice or half the fish being caught four times, even if some proportion of the population is tagged. Only tightly controlled studies with complete angler censuses, such as Burkett et al. (1986), could fully describe how many times each fish was caught, and so provide an accurate description of the relative contribution of multiple catches to the total catch. Unfortunately, complete censuses are not practical for most fisheries.

At first glance, it may seem that the recycling rate within a fishing season could be readily obtainable from tagging data. However, the process of determining how many times each fish was caught based on tag return data requires knowledge of the frequency distribution of angling selectivity among all individual fish in the population, and voluntary tag return data will generally be such a sparse sample of actual angling activity that it would be functionally impossible to use such data to accurately determine the selectivity frequency distribution. In this context, we do not mean that we must identify the selectivity for fish with a particular trait; rather, we need to define the relative frequency of each value of selectivity in the population of interest. This selectivity distribution must account for both contact selectivity and availability (Maunder et al. 2014). In a recreational fishery, contact selectivity can be viewed as the relative likelihood of being caught when encountering a lure or bait, which can be influenced by combinations of multiple factors including individual variations in behavioral traits (Tsuboi and Morita 2004; Philipp et al. 2009), angling gear (Wilson et al. 2015), size distributions and sex ratios (Schultz 2003; Myers et al. 2014), and environmental conditions (Heerman et al. 2013). This distribution generally cannot be determined from tag return data because any attempt to define the selectivity distribution would be overparameterized and coupled with noise from incomplete tag return data. In the context of estimating recycling rate, this means that there will be many different selectivity distributions that could explain the observed data, with no way to discern which of the possibilities is the most likely one. Therefore, any attempt to compute the recycling rate will be dependent on assumptions about the selectivity frequency distribution, and any assumed distribution will be difficult to verify with complete confidence.

Our objective here is to develop a useful model to estimate the recycling rate from parameters that are readily attainable. As with many fishery models, the choice of assumptions may be influential. In particular, assumptions about the shape of the angling selectivity frequency distribution must be explored. We will present a general solution to estimate recycling rate that can be numerically solved for any selectivity frequency distribution. From this general solution, we will derive four estimators based on some simple assumed selectivity distributions. We will then apply these models to Smallmouth Bass *Micropterus dolomieu* data from Mille Lacs Lake, Minnesota, and evaluate the robustness of these estimators by comparing them to the recycling rate estimated using the general solution and a more realistic presumed selectivity distribution. Additionally, we will examine the effects of hooking mortality of released fish on model integrity.

To improve readability, the mathematical development of our solutions is described in the online supplemental appendix for this article. Also for simplicity, since we are interested in parameter values at $t = 1$ season, time references used in the appendix will be dropped from equations in the paper itself (e.g., $C(t)$ will be presented as C). Data fitting and simulations were conducted using the SciPy library (Virtanen et al. 2020) for the Python programming language (Van Rossum 1995).

THE GENERAL SOLUTION

The ideal way to obtain the recycling rate in a fishery would be to track multiple captures of a tagged subsample of the population with 100% of the tags reported. Assuming that tagged and untagged fish are equally vulnerable to angling, the recycling rate is the total angling catch of tagged fish, including recaptures, divided by the number of individual tagged fish caught not including recaptures. However, if only some of the tags are reported, we no longer know either the total catch of tagged fish or the number of individual tagged fish caught, and some other method must be found because calculating a direct quotient is no longer possible.

For mathematical convenience, development of this method required us to use some familiar concepts in unfamiliar ways. First, we need a definition of seasonal catchability, which we designate as Q. The standard definition of catchability, q, is the proportion of the population caught using some gear with one unit of sampling effort (Arrenguín-Sánchez 1996). It follows that the number of fish caught with effort E is NqE, where N is the population size. We define the seasonal catchability as the proportion of the population caught in a season of angling, or $Q = C/N = qE$, where E now represents effort for the entire season. Selectivity, s, describes the relative vulnerability of distinct segments of a population to a specific gear (Cadrin et al. 2015). The catchability of fish in the ith segment of the population is $s_i q$. Ordinarily, the selectivity of the identified segments varies around unity such that the average catchability for the population is q. To develop our models, we limited values of selectivity to between 0 and 1, and based the catchability of the ith fish as some proportion of the fish with maximum catchability, $q_i = s_i \cdot q_{\max}$. Treating the season as a single unit of effort, we defined a seasonal maximum catchability, $\varphi_{\max}$, such that the ith fish now had a seasonal catchability of $s_i\varphi_{\max}$. The individual catchability for each fish in the population was determined by a frequency distribution of the selectivities, which we expressed as a probability density function $h(s)$.

Using our definitions, we derived the fraction of fish caught by angling exactly i times (see appendix for details) as

$$f_i = \frac{\varphi^i_{max}}{i\,!}\int_0^1 e^{s\varphi_{max}} s^i h(s) ds. \tag{1}$$

Unfortunately, there are many possible $h(s)$ that could produce any observed tag return data, but the data will almost always be insufficient to choose the appropriate $h(s)$ (See discussion of λQ below). At a minimum, it would require very high catches and very high tag reporting rates by anglers such that most tagged fish that were caught were reported multiple times. If $h(s)$ were known, the fractions of fish caught i times can be numerically determined, and the recycling rate is

$$R = \frac{\sum_1^{i_{max}}\left(i * f_i\right)}{1-f_0} = \frac{Q}{1-f_0}, \tag{2}$$

where Q is our seasonal catchability coefficient. Assumptions of this model include that the population is constant across the season, meaning no natural or fishing mortality, and that the selectivity of each fish is constant across the season.

We developed solutions for four sets of assumptions about the shape of the selectivity frequency distribution. The first two included assuming that all fish were vulnerable to angling and had either equal selectivities or uniformly distributed selectivities (all selectivities between 0 and 1 are equally likely). We also considered the assumption that an unknown proportion of the population is not vulnerable to angling, while the remaining proportion has either equal or uniformly distributed selectivities.

EQUAL SELECTIVITIES

In the simplest possible case, we assume that all fish are equally catchable. The recycling rate, R, is

$$R = \frac{Q}{1-e^{-Q}}. \tag{3}$$

Recall that Q is the seasonal catchability, C/N, where C is the catch and N is the population size. No tag return data is needed to solve for the recycling rate, and confidence intervals can be obtained through bootstrapping. It is noteworthy that this equal selectivity estimate of recycling rate is the minimum possible estimate because if any portion of the population becomes less catchable, the remaining portion of the population must be caught more often to have the same catch over the season. Also, under this assumption, R approaches Q as Q increases, and essentially becomes equal to Q when Q is greater than three. That R approaches Q should make sense intuitively because as catch increases, more individuals contribute to the catch. At some point, the catch is so high that every individual will have been caught at least once. At that point, $f_0 = 0$, and equation 2 becomes $R = Q$.

The assumption of equal selectivities leads to a clean and simple model. However, tag return data from small census experiments suggest that equal selectivity is unlikely (Burkett et al. 1986; Tsuboi and Morita 2004).

UNIFORMLY DISTRIBUTED SELECTIVITIES

Another selectivity frequency distribution that offers a tidy solution is uniformly distributed selectivities, where all selectivities between zero and one occur with equal probability and $\varphi_{\max} = 2Q$. In this case, the recycling rate resolves to

$$R = \frac{2(Q)^2}{2Q-\left(1-e^{-2Q}\right)}. \tag{4}$$

Once again, no recapture data are required, and uncertainty can be assessed through bootstrapping. With this model, R is always greater than Q because some individuals have very low selectivities, virtually assuring that some fish will never get caught.

DISTRIBUTIONS WITH UNAVAILABLE FRACTIONS

In the two previous scenarios, all fish were assumed to be equally available to angling, even if angling selectivities were unequal. But selectivity can be partitioned into contact selectivity (our angling selectivity) and population selectivity, or availability (Maunder et al. 2014). Some fish will experience lower availabilities because angler effort may not be distributed equally across all habitats. For example, in the Lake Mille Lacs Smallmouth Bass fishery, most effort is concentrated on rock structure in water less than 4 m deep, with very little directed effort in deeper water, even though divers observe bass at depths of 8 m or more (T. Jones, personal observations). While these deeper bass are sometimes incidentally caught by Walleye *Sander vitreus* anglers, they are subject to much less targeted angling and are assumed to be less vulnerable.

Thus, models that explore unequal availability also need to be considered.

If we let the proportion of fish that are available be p, the unavailable proportion is $(1 - p)$. Now, the catchability coefficient of the available proportion is Q/p. For equal catchabilities, the recycling rate becomes

$$R = \frac{Q/p}{1 - e^{-Q/p}}. \tag{5}$$

When p is less than 1, the recycling rate increases because the remaining fish must be caught more often to produce the observed catch.

However, p is unknown. To estimate p, we can fit tag return data to a set of equations describing g_i, the fraction of tagged fish reported i times. When the vulnerable portion is assumed to be equally catchable,

$$g_0 = pe^{-\lambda Q/p} + (1 - p), \tag{6}$$

and for $i > 0$

$$g_i = p\frac{1}{i!}e^{-\frac{\lambda Q}{p}}(\lambda Q/p)^i, \tag{7}$$

where λ is the tag reporting rate, or the likelihood that an angler reports a tagged fish that has been caught.

Similarly, for uniformly distributed catchabilities among the vulnerable proportion, the recycling rate is

$$R = \frac{2(Q/p)^2}{\left(\frac{2Q}{p}\right) - \left(1 - e^{-2Q/p}\right)}, \tag{8}$$

and p is found by fitting

$$g_0 = \frac{p^2}{2\lambda Q}\gamma(i + 1, 2\lambda Q/p) + (1 - p) \tag{9}$$

$$g_i = \frac{p^2}{2\lambda Q}\frac{1}{i!}\gamma(i + 1, 2\lambda Q/p) \tag{10}$$

where γ is the lower incomplete gamma function (Weisstein 2021)

$$\gamma(x, y) = \int_0^y w^{x-1}e^{-w}dw. \tag{11}$$

Both models allow utilization of tag return data, but also require some assumptions about the tagged population. These include equal vulnerability to angling of tagged and untagged fish, tags are not lost, and no recruitment or mortality occurs. The common assumption that all tags are recognized and reported is not necessary here. If all tagged fish were reported, estimating recycling rate would be trivial because the exact number of times each fish was caught would be known.

EVALUATING MODEL PERFORMANCE USING "PLAUSIBLE" SELECTIVITIES

Ideally, we would be able to compare our four simple models to the actual recycling rate derived from a known selectivity frequency distribution from a real fishery. With a known distribution, the actual recycling rate could be estimated by solving the integral of equation (1), or by numerical approximation if the integral lacks a closed-form solution. But as we have said, the tag reporting data cannot provide us with this distribution. Since the actual distribution of selectivities is unknown, we used a plausible selectivity distribution function as a proxy to estimate the "true" recycling rate.

Clearly, the distributions of selectivities among individuals in a population are more complex than the simple distributions of our models. The willingness of a fish to take an angler's offering is unlikely to vary in a clean, linear fashion. It seems reasonable that the selectivity frequency distribution of fully available fish should have some type of dome-shaped distribution. It also seems reasonable that the selectivities of the less vulnerable individuals should vary as a nonlinear gradient rather than "on or off" as in our models with unavailable fractions.

We created a plausible selectivity distribution for the Mille Lacs Lake Smallmouth Bass fishery. We have qualitative evidence from scuba diving and Walleye angling that some portion of the population lives in deeper water than most bass anglers are willing to fish (T. Jones, personal observation). And we have observed higher bass densities in shallower water while diving and in fall gill net sampling (Minnesota Department of Natural Resources, unpublished data). We assumed that approximately 75% of the fish would be considered fully vulnerable to angling with some form of dome-shaped selectivity frequency distribution, and 25% will be less accessible, with much lower selectivities. We used these assumptions to develop a cubic equation that served as a plausible, but not proven, selectivity distribution function (Figure 1).

The true recycling rate was estimated using this plausible selectivity distribution. Using available catch and abundance data (Table 1), we ran 1,000 simulated fishing seasons. The number of times each fish was caught in each season was determined by randomly selecting fish based on each fish's probability of capture until the simulated catch reached the predetermined total catch of 3,876, which was the number of tagged fish multiplied by Q. A caught fish had a probability of being reported of λ, which varied as a Poisson distribution for each season. We assumed that C and N were known so that all variation in the recycling rate was from chance differences in the number of times each tagged fish

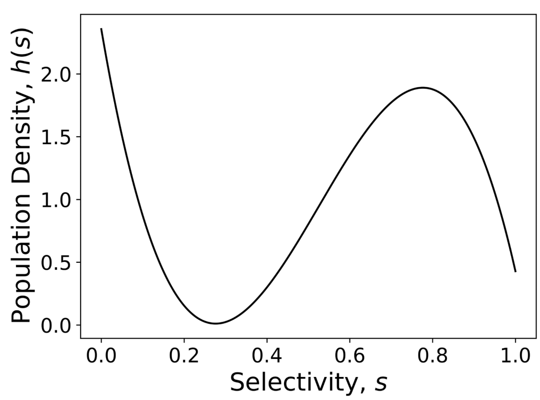

Figure 1. A "plausible" selectivity distribution function for Smallmouth Bass in Lake Mille Lacs, Minnesota.

Table 1. Parameters used to estimate recycling rates of Smallmouth Bass in Lake Mille Lacs, 2017. MN DNR = Minnesota Department of Natural Resources. Parameter abbreviations are as follows: $h(s)$ is the selectivity frequency distribution, C is the catch for the season, N is population abundance, T is the number of fish tagged.

Parameter	Mean	Distribution	Source
Population, N	67,000	SE = 5,000	Schwarz 2018
Catch, C	125,000	SE = 10,000	Beyerl 2018
Tagged fish, T	2,084	n/a	Schwarz 2018
Tags reported once, T_{r1}	233	Poisson	MN DNR records
Tags reported twice, T_{r2}	7	Poisson	MN DNR records

was caught and whether each caught fish was reported. We estimated that the true recycling rate for Smallmouth Bass in Lake Mille Lacs was 2.53.

We compared the true recycling rate to our four model estimates (Table 2). The two models in which all fish were assumed vulnerable compared favorably with the true rate. The equal selectivity model produced a slightly lower recycling rate because it was a minimum estimate. The recycling rate from our uniformly distributed model was nearly identical to our true rate, despite having been generated from a very different selectivity distribution. These results suggest that the estimate of recycling rate is robust to assumptions about $h(s)$. The two models with unavailable fractions produced much higher recycling rate estimates. In both cases, fitting our tag return data produced small estimates of the available proportion, p, which greatly inflated the recycling rates. The tag reporting rate, λ, was 6%, which was too low to provide adequate fitting of equations (7) and (10).

To further investigate the effect of λ, 1,000 simulations were repeated for the plausible selectivity distribution model for each value of λ ranging from 0.05 to 1 in increments of 0.05. The mean recycling rate was 2.51 with a bootstrapped 95% confidence interval of 2.46 to 2.56. We then compared the true recycling rates to recycling rates generated by our four simplified models, which included equal selectivities and uniformly distributed selectivities, each with and without an unavailable fraction. Again, 1,000 simulated seasons were run for each model for each value of λ from 0.05 to 1. For these simulations, C and N were varied according to observed measurement error (Table 1). Bootstrapped 95% confidence intervals were approximately the mean ± 0.35 for each of the four models, and these confidence intervals included the true recycling rate for all models for all values of λ, except the equal selectivity model when λ was low (Figure 2). Recycling rates from the uniformly distributed selectivity models were within 1% of the true rate for all λ.

As expected, the models without unavailable fractions were constant over the range of λ because recycling rates from these models did not depend on tag returns. Unexpectedly, the uniformly distributed model with an unavailable fraction also did not vary with reporting rate. This was because the fitted value of p was always equal to 1, which was an artifact of the choice of the plausible selectivity curve and does not represent a failure of the model. Other selectivity curves may yield nontrivial fits of p to tag return data.

The fitted estimate of p for the equal selectivity model with unavailable fraction was approximately 0.7 at $\lambda = 0.05$, but approached unity as λ increased (Figure 2). This model matched the plausible selectivity model better than other models when the tag reporting rate was higher than 60%. While such reporting rates have been documented in some cases in conjunction with high-reward tags (Meyer et al. 2012), lower reporting rates are more common (e.g., Green et al. 1983; Fielder 2014). The reporting rate for tagged Smallmouth Bass in Lake Mille Lacs was only 6%, leading to doubt about the utility of models with unavailable fractions.

Our results demonstrated that estimates of recycling rate are quite robust to assumptions about the exact shape of the selectivity frequency distribution when all fish are considered vulnerable. This is fortunate because it allows the use of a simple model to approximate recycling rate without serious concerns about differences between our plausible selectivity frequency and the true, but unknown, selectivity frequency. Our preferred model is the uniformly distributed model without an unavailable fraction because of its simplicity, nonreliance on tag return data, and very good agreement with the recycling rate generated by our plausible selectivity distribution.

DEPENDENCE OF P ON λQ

The quantity λQ is a recurring feature of equations (6), (7), (9), and (10). This is the product of the angler tag reporting

Table 2. Estimates of recycling rate for Smallmouth Bass on Lake Mille Lacs, 2017. Confidence intervals were bootstrapped. Parameter abbreviations are as follows: $h(s)$ is the selectivity frequency distribution, C is the catch for the season, N is population abundance, T is the number of fish tagged, and T_{ri} is the number of tagged fish caught and reported i times.

	Recycling rate		Available fraction		
Model	Mean	95% CI	Mean	95% CI	Parameters required
Plausible selectivity	2.53	2.20–2.95	1	NA	$h(s)$, C, N, T
All fish available ($P = 1$)					C, N
Equal selectivity	2.21	1.92–2.57	1	NA	
Uniformly distributed selectivity	2.55	2.19–2.99	1	NA	
Unavailable fraction ($P < 1$)					C, N, T, T_{ri} for $i \in (0, i_{max})$
Equal selectivity	16.31	12.05–21.18	0.12	0.10–0.13	
Uniformly distributed selectivity	9.15	6.61–12.22	0.22	0.19–0.26	

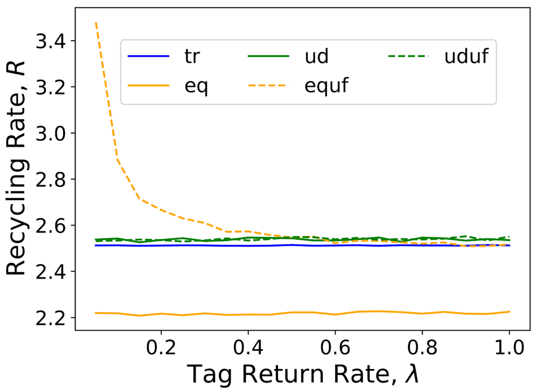

Figure 2. Recycling rates as determined using the "plausible" selectivity distribution and four solvable models. Models are abbreviated as follows: tr, the "true" recycling rate using the plausible selectivity distribution; eq, equal selectivity; ud, uniformly distributed selectivity; equf, equal selectivity with unavailable fraction; uduf, uniformly distributed selectivity with unavailable fraction. Bootstrapped 95% confidence intervals included ±0.05 for the true recycling rate, and approximately ±0.35 for each of the other models.

rate and the seasonal catchability coefficient, and is equal to the ratio of the number of reported tags, T_r, to the number of tags applied, T, which is often referred to as the tag return rate (e.g., Murphy and Taylor 1991). Thus, λQ can be estimated directly from tag return data as

$$\lambda Q = \frac{T_r}{T}. \tag{12}$$

This is meaningful because increases in either λ or Q would result in similar increases in the number of reported tags, which will lead to estimates of p that are both more accurate and more precise (Figure 3). This insight leads to two interesting sidenotes. First, if we treat T_r as a Poisson variable, the quantity λQ can also be treated as a Poisson variable when estimating uncertainty around p. This may be simpler than bootstrapping. Second, indirect methods such as reward-tagging may be used to estimate λ (Pollock et al. 2001), providing estimates of Q and R without the need to conduct a creel survey.

To investigate the behavior of estimates of p over the entire range of λQ for both of our models with unavailable fractions, we again used simulations based on the 2017 Lake Mille Lacs Smallmouth Bass fishery (Table 1). For each simulation, Q was set at $C/N = 1.86$, and λ ranged from zero to one in increments of 0.01. For each λ, we simulated 1,000 season each for p values of 0.2, 0.5, and 0.8. Simulated catch and reporting histories were fitted to equations (6) and (7) to determine an estimate of p for each simulated season.

For the equal selectivity model, we found that when λQ was too low, p could not be reasonably estimated because the distribution of returned tags was insufficient to describe the expected catch history (Figure 3A). In 2017, λQ in the Mille Lacs fishery was 0.11. At such a low value, the model had little chance of correctly estimating the unavailable fraction. Estimated values of p were often nonsensical at low λQ since p cannot be larger than 1. As λQ increased, estimated p approached assigned p, and confidence in estimated p improved.

Performance for the uniformly distributed selectivity model (Figure 3B) was poor for all values of λQ. Although estimates of p were much more consistent at low λQ than for the equal selectivity model, p was consistently underestimated. This occurred because the model essentially considered some fish that were available with very low selectivities as fish that were unavailable to angling. Underestimated values of p result in overestimates of recycling rate. It may perform adequately if Q is much higher, although such high catchabilities are likely rare.

These simulations further erode our confidence in models with unavailable fractions.

MODEL BIASES

Our models assumed that there was no hooking mortality of released fish. However, hooking mortality in catch-and-release fisheries is common and has been documented for many species (Muoneke and Childress 1994). The effect of a constant hooking mortality rate was examined by modifying our simulations such that every time a fish was caught, there was some probability that it would die and not be available for subsequent recapture. Estimates of recycling rate are biased high when fishing mortality is ignored (Figure 4). The bias is not great, however. Even at 20% hooking mortality, the recycling rate for the uniformly distributed selectivity model is still higher than the recycling rate from the equal selectivity model with no hooking

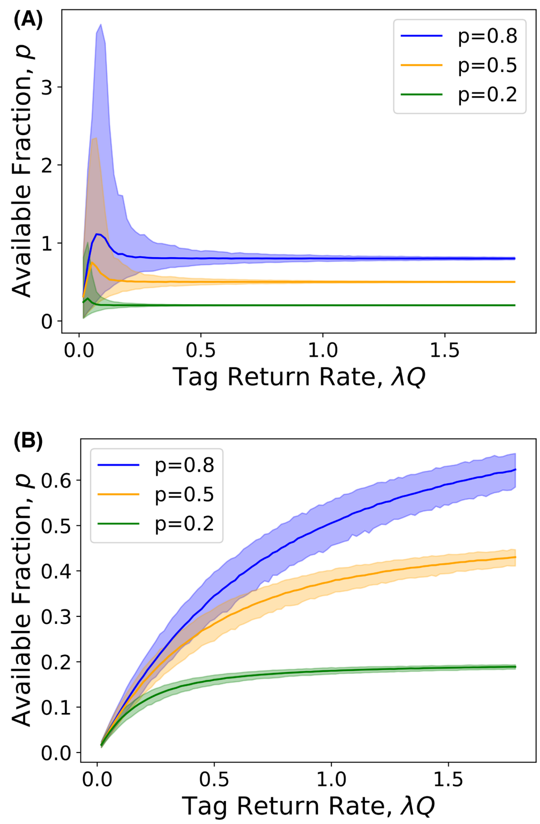

Figure 3. Estimates of the proportion of fish vulnerable to angling, p, obtained by fitting simulated tag return data across a range of λQ for p values of 0.2, 0.5, and 0.8. for (**A**) the equal selectivity model with unavailable fraction and (**B**) the uniformly distributed selectivity model with unavailable fraction. Simulations were based on catch and abundance estimates for the 2017 Smallmouth Bass fishery in Mille Lacs Lake, Minnesota. Lines are means of estimates of p and shaded intervals include 95% of estimates of p.

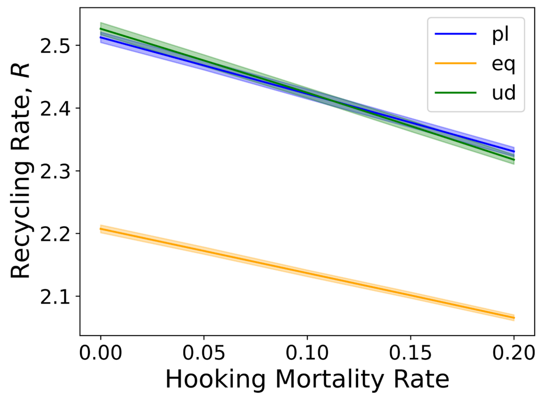

Figure 4. The effect of hooking mortality on recycling rates for Smallmouth Bass in Lake Mille Lacs, Minnesota. Recycling rates were calculated using the plausible selectivity distribution, pl; the equal selectivity model, eq; or the uniformly distributed model, ud. Lines are mean estimate and shaded intervals include 95% of estimates.

mortality. The degree of bias was dependent on both the hooking mortality rate and the shape of the selectivity frequency distribution used in the simulation. The selectivity distribution is important because fishing mortality will tend to decrease the abundance of the most catchable fish first. Since the catch is fixed in our simulations, the subsequent recaptures of a highly catchable fish must be replaced with catches from less catchable fish, which increases the number of individual fish caught. If an equal selectivity distribution is used, fewer additional fish are required to replace the recaptures of killed fish. For unavailable-fraction models, fishing mortality will also reduce the number of tags reported, leading to lower values of λQ, poorer estimates of p, and poorer model performance. Future work may improve our models to accommodate fishing mortality.

Our models with an unavailable fraction depend on tag return data, which can be affected by tag loss. Some tag loss may occur almost immediately after tagging, but tags may also be shed over a longer period of time (Cowen and Schwarz 2006). Additionally, the rate of tag shedding may also vary by individual attributes, such as age (Rotella and Hines 2005). Significant tag loss will manifest itself as an underestimate of λQ, because fish that were tagged simply will not be recognized, and the tag return rate will be biased low, even if the tag reporting rate is high. We have shown that the accuracy and precision of estimates of p will break down at lower values of λQ, which could cause positive or negative bias. Rather than attempt to characterize tag loss through additional simulations, we view the added complexity of tag loss as another argument in support of abandoning the tag-dependent models.

We assumed that the selectivities and closely related catchabilities of individual fish were constant across a season. Some authors have found vulnerability to angling can be reduced by the experience of being caught (Askey et al. 2006; Hessenauer et al. 2016), which would suggest that the selectivity of the most vulnerable fish can decline if fishing effort is sufficient. However, Tsuboi and Morita (2004) found that char *Salvelinus* spp. that had been previously caught were the most likely to get caught in subsequent fishing events. Selectivity and catchability may also be influenced by numerous biotic and abiotic factors (VanDeValk et al. 2005; Kuparinen et al. 2010; Heerman et al. 2013). However, since our estimates of recycling rate were robust to changes in the selectivity distributions, and our catchability, Q, incorporates periods of high and low catchabilities within a season, some plasticity of the selectivity frequency distribution within a season should not create large errors in the estimates.

CONCLUSIONS

To the best of our knowledge, no one has published a method to quantify the increased catch realized through catch-and-release fishing. Recycling is often cited as the average number of times each fish is caught (Schill et al. 1986; McCormick 2016), but these are estimates of seasonal catchability rather than recycling rate. Proof of recycling exists when catch exceeds abundance, but our methods allow for estimating recycling rate even when catch is well below abundance. The recycling rate of a fishery will certainly be noteworthy to anglers interested in promoting catch-and-release of their favorite species. It may also be a useful tool to quantify the positive trade-off that harvest-oriented anglers will receive for releasing their catch, which could increase acceptance of otherwise unfavorable regulations.

We recommend applying the uniformly distributed selectivity model in most circumstances. Estimates of recycling were robust to different assumptions about the distribution of selectivities, which favors the use of simpler models that do not rely on fitting tag return data. Managers considering use of a model involving unavailable fractions should first verify that λQ is sufficiently large to generate reliable estimates of the proportion of fish available to anglers. The equal selectivity model is also easy to apply but likely underestimates the recycling rate because it is a minimum value.

Finally, managers are encouraged to explore recycling rates for any selectivity distribution functions that they think might apply to their fishery. Recycling rates for any known or imagined selectivity distribution function can be numerically approximated using Python scripts available at https://bit.ly/3zQiYBb.

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ORCID

Thomas S. Jones https://orcid.org/0000-0001-8931-0176

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.

Appendix S1 Supporting Information. AFS