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# Are removal-based abundance models robust to fish behavior?

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ABSTRACT

Removal methods are some of the most common statistical tools for estimating fish abundance in streams and lakes, yet they are prone to produce biased estimates when the assumption of constant capture probability is violated. In response, numerous authors have modified the classic removal models to control for non-constant capture probability. A variety of fish behaviors can cause capture probability to vary across individuals or over time, such as dominance hierarchies, escaping capture or persistent individual differences in capture probability due to activity or aggression; yet knowing exactly which behaviors may affect capture probability is generally unknown. We assessed the robustness of five removal models (i.e., the Leslie model, three behavior-dependent models and a density dependent capture probability model) and their ability to provide consistently accurate and precise abundance estimates irrespective of the exhibited behavior. We fitted each model to catch data generated from five behavioral models that mimicked a range of animal behaviors in a closed population. Additionally, we evaluated the improvements that can be gained by including marked fish in the removal process and in that case, compared estimation models with a Peterson mark-recapture estimation. Results indicate that no single removal model is robust to non-constant capture probability, however, the density-dependent capture probability model performed moderately better than other models when only removal data were used. We found that the addition of marked fish results in a substantial improvement in accuracy and precision across all removal models when mark-recapture assumptions are met. However, these improvements diminished substantially when mark-recapture assumptions were violated. Due to the difficulties in assessing assumptions, our findings suggest that including marked fish in the removal process may unknowingly reduce accuracy and precision of initial abundance estimate and that this type of experimental design should be avoided in many instances.

## 1. Introduction

Removal methods (also referred to as depletion or catch-effort methods) are conceptually straightforward: the catch-per-unit of sampling effort (CPUE) at each successive sampling event should decline as animals are cumulatively removed from each previous sampling event. These methods are appealing because they are intuitively simple and require relatively few data to provide abundance estimates (Smith and Addison, 2003; Yamakawa et al., 1994). It is recognized that bias in abundance estimated using removal methods can be substantial in certain cases (Bohlin and Sundström, 1977; Hilborn and Walters, 1992; Mahon, 1980; Peterson and Cederholm, 1984; Riley and Fausch, 1992), particularly when assumptions are violated, yet these models continue to be among the most common means of population assessment, particularly in small, closed populations.

The primary assumption in most removal models is constant probability of capture. It was initially assumed that variation around the mean decline in CPUE was caused by random variation. However subsequent work has demonstrated that there can often be transitory (Benejam et al., 2012; De Gisi, 1994; Kelso and Shuter, 1989; Peterson and Cederholm, 1984) or persistent (Kelso and Shuter, 1989; Schnute and Fournier, 1980) changes in capture probability, can lead to substantial bias ranging between 30 and 50% in abundance estimates (Hilborn and Walters, 1992). It is most often observed that capture probability declines over the course of a removal experiment, leading to declines in catches and negative bias (underestimates) in population abundance.

A variety of fish behavior patterns could plausibly lead to changes in capture probability. For example, changes in aggregate capture probability may be due to intrinsic differences in behavior among individuals, leading some fish to have a higher probability of capture than others, so that the most 'catchable' fish are removed first (Carle and

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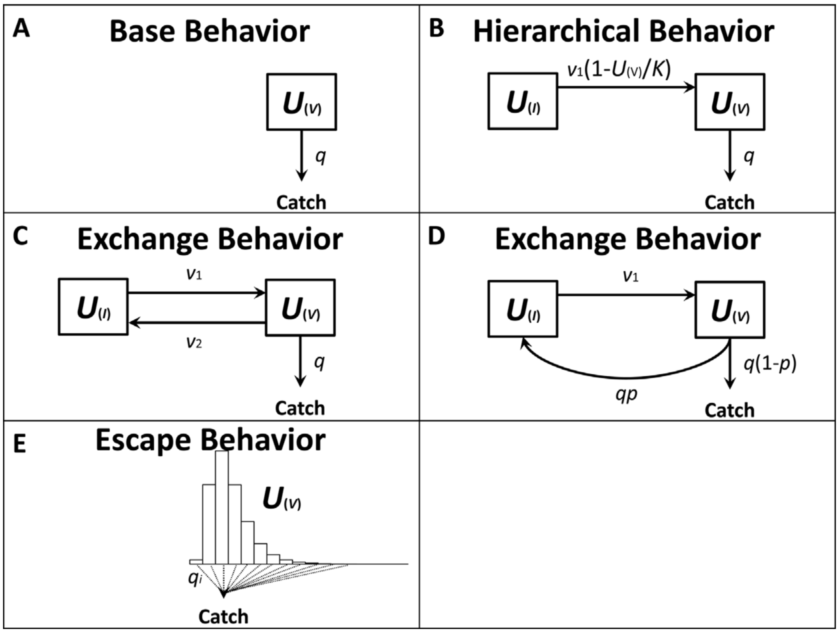


**Fig. 1.** Graphical representation of each simulated behavioral model affecting the depletion process (and marking where specified). In all models, only vulnerable fish are available to be captured and invulnerable fish may return to the vulnerable state at a density dependent rate.

Strub, 1978; Ricker, 1975; Wyatt, 2002). As aggregate capture probability among remaining fish declines with each removal period, estimated abundance will decrease, causing negative bias. Alternately, fish may directly react to previous capture events in which they escaped capture, resulting in a different aggregate capture probability across sampling events (akin to a 'trap response'; Pollock et al., 1984). If fish avoid the gear after escaping, this also lowers aggregate capture probability in later sampling periods, also leading to negative bias in abundance. Finally, aggregate capture probability may be directly linked to abundance, so that capture probability declines with abundance, as in schooling populations (Mantyniemi et al., 2005; Ricker, 1975). In this case, aggregate capture probability will become progressively higher as fish are removed, leading to positive bias in abundance. In most sampling situations, one or several behavioral mechanisms may be operating, but the dominant mechanism will vary across populations and sampling situations. Regardless of the exact behavior(s) involved, this suggests that the primary reason why estimation models have difficulty estimating abundance when fish react to the removal process is because there is a proportion of the population not available to be sampled. While many fixes to the assumed problems of removal models have been proposed and tested (e.g., Pollock et al., 1984; Schnute, 1983; Wyatt, 2002), there have been no evaluations of model performance across a series of behavioral and physiological mechanisms that may cause changes in capture probability. The key question is whether these behavioral patterns will lead to significant bias in abundance and whether there is a single model that is robust to these violations of capture probability.

The purpose of most removal experiments is to estimate abundance, regardless of the behavior of fish being captured. An alternative method to potentially reduce bias in estimated abundance is to mark fish prior to the removal process and jointly estimate the removal process of marked and unmarked fish (Ricker, 1975). Using marked fish in removal studies may help address non-constant capture probability and bias-correct abundance estimates (Yip and Fong, 1993). However, mark-recapture models also have several strong assumptions, which can be difficult to test and address (Ricker, 1975; Schwarz and Seber, 1999); if the same behaviors affect fish in the marking process as in the removal process, validating one method with the other may be profoundly misleading. If marking fish is to be used to address removal estimation bias, it is important to understand the conditions necessary to ensure results are accurate and unbiased.

The objectives of this work are to show how unpredictable, but likely, fish behaviors will impact removal patterns and compare the estimation performance of several estimators across a variety of fish behaviors. Our hope is to identify a single estimator that reliably estimates abundance regardless of fish behavior. Simulated behaviors include a base model where all fish are equally vulnerable (Leslie and Davis, 1939); hierarchical dominance where only dominant fish are available; vulnerable exchange where fish randomly move between vulnerable and invulnerable states (Cox et al., 2002); escape where fish that randomly escape capture become invulnerable for a time; and individual behavior where each fish has a unique capture probability. We also investigate how using marked fish in removal experiments affects abundance estimates, even if assumptions of mark-recapture may be violated due to the same behaviors affecting the removal process. Through this process, we will determine if there is a single removal model that provides a relatively accurate and precise abundance estimate regardless of underlying animal behavior.

## 2. Methods

The following two sections describe five behavioral reactions to the capture process. Each of these individual behaviors will lead to changes in aggregate capture probability over capture events. In Section 2.3, we present the five estimation models that were used to estimate the initial abundance of the simulated population ($N_0$). Three scenarios were run: (1) where all fish are unmarked; (2) where a random selection of fish were marked prior to the removal process and all assumptions of mark-recapture were met; and (3) where fish were marked prior to the removal process, but were subject to the same behaviors of the removal process. We evaluated models by fitting each estimation model to catch time series generated using each of the simulated behaviors. We assume removal experiments are sufficiently short to not be affected by natural mortality and all losses are due to the removal process.

### 2.1. Behavioral models assuming marks randomly allocated

Five behavioral models were simulated, each depicting a particular behavioral response to the capture process (shown graphically in Fig. 1). To enhance realism of the simulation models, data were generated using individual-based models, where the fate of each individual in each time step is dictated by a stochastic parametric function. Each of the behavioral models is fully described in Table 1 and all symbols are defined in Table 2. Parameters used in each simulation model were