



A length-based mark-recapture model for estimating abundance and recruitment: Removing bias due to size-selective capture gear

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ABSTRACT

We describe an unbiased length-based, age-structured mark-recapture (LAMR) model for estimating length-based abundance and recruitment of fish populations. Many mark-recapture studies employ capture gear that is size-selective, leading to a larger and faster growing marked sub-population with a different capture probability than the unmarked sub-population, resulting in a basic violation of assumptions for many mark-recapture models. Persistent differences in marked and unmarked individuals are estimated in our model using growth-type group accounting. Simulation-evaluation results indicate that the model produces largely unbiased estimates of recruitment and abundance across a range of sampling scenarios and population life-history types, and is robust to growth parameter misspecification. However, in older, slow growing populations, the model is prone to 'smearing' of recruitment estimates across early year-classes. The LAMR model is applied to data from multiple wild populations of rainbow trout to estimate recruitment and abundance. Overall, results indicate that the LAMR model addresses shortcomings associated with using size-selective gear in mark-recapture studies to produce reliable estimates of recruitment and size-based abundance.

1. Introduction

Many management actions are predicated on an accurate assessment of the abundance of animals being managed. Changes in the numbers of organisms strongly determine rates of predation, food consumption, competition and reproduction in ecosystems (Carpenter and Kitchell, 1996), which in turn may result in future changes in abundance resulting from density dependent survival, growth and reproductive success. In many organisms with indeterminate growth (e.g. fish, reptiles), all of these rates are typically size dependent (Werner and Gilliam, 1984; Begon et al., 1996; Miller and Rudolf, 2011) and thus it is additionally important to assess both total and size-structured abundance over space and time when predicting the effect of one or several species on an ecosystem (De Roos et al., 2003). With this in mind, any management decision that affects the size-structure of one or a group of species may have effects on the ecosystem as a whole (Rochet and Benoit, 2012).

Estimates of abundance are often obtained using depletion or mark-recapture models. Depletion models estimate abundance by monitoring how catch or other abundance indices change over time with a known amount of harvesting effort. Mark-recapture studies

estimate abundance by evaluating the change in the number of marked animals over multiple capture occasions. Information from the marked subset of the population is then used to estimate capture and/or survival probabilities, which are then used to make inferences about the entire population (Pine et al., 2003). Models that combine both methods do exist in some limited contexts (Maunder and Deriso, 2003; Polacheck et al., 2006; Coggins et al., 2006; Cadigan, 2016), but many simply use tags to solely estimate movement or spatial distribution (e.g. Whitlock and Mcallister, 2009), rather than absolute abundance. True combinations of the two methods are very rare (although see Polacheck et al., 2006).

Animals within a population grow at different rates (Wang et al., 1998; Sinclair et al., 2002) and it is generally believed that growth variation among individuals is persistent (Sainsbury, 1980; Parma and Deriso, 1990; Mangel and Stamps, 2001); fast growers consistently grow faster than slow growers. It was recognized early in fisheries research that fast growers are differentially selected by fisheries leading to skewed size-at-age distributions (Lee, 1912; Ricker, 1969; Sinclair et al., 2002). When using size-selective sampling gear, differential growth leads to differential capture probability, which can bias certain assessment models like age- or size-structured depletion models

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(Sainsbury, 1980; Walters and Martell, 2004; Catalano and Allen, 2010). In mark-recapture experiments, fast growers may be better represented in the marked sub-population because they were more likely to be initially captured and tagged. Failure to account for differential capture probability of marked and unmarked animals is a violation of a basic assumption of mark-recapture models (Seber, 1982) and will result in bias of total population abundance estimates (van Poorten et al., 2017). We are not aware of any method for estimating size-structured abundance that explicitly tracks a persistent difference in body growth between marked and unmarked animals in a mark-recapture model.

The key to addressing bias associated with persistent growth variation is explicitly tracking groups of individuals with different growth trajectories. This process can be accomplished using an individual-based model (IBM), but these models are computationally intensive. Growth-type-group (GTG) models are a useful approximation to IBMs yet are still able to replicate cumulative size-based mortality effects on size structure. GTG models stratify age-classes into groups with a specific growth trajectory set at a fixed deviation from the mean growth function and the abundance of each GTG is tracked over time so changes in the size structure persist through time (Walters and Martell, 2004). The GTG accounting method has been shown to effectively address size-selective removals of fish in length-based models (Parma and Deriso, 1990; Taylor et al., 2005) and may be useful in directly estimating the effects of differential growth rates in mark-recapture studies between marked and unmarked individuals. The utility of GTG models to overcome the problem of variability in capture probabilities within year-classes due to differential growth rates in mark-recapture models is obvious, yet no models have been developed to date.

We describe a method for estimating size- and age-structured abundance using a method we call length-based, age-structured mark-recapture (LAMR). This method takes advantage of mark-recapture data by using marked individuals to help estimate selectivity and capture probability, while also estimating recruitment into each year-class of the total population. We focus on assessment of fish populations, but the method could be used for any species with indeterminate growth. Our method explicitly accounts for size-selectivity of various capture gears and appropriately accounts for selective removal of fast growing animals from the population. It is not necessary to include multiple capture gears or removal methods at the end of each season; their inclusion here is used to demonstrate the flexibility of the model and to match the data provided in our case study. While the model could take advantage of individually marked animals, we chose to condition the model on batch-marking. We simulation-tested the model to evaluate relative error in estimated parameters and model performance against more commonly used Jolly-Seber models. Finally, we apply the LAMR model to eight wild rainbow trout (*Oncorhynchus mykiss*) populations from lakes in south-central British Columbia to estimate recruitment and size-structured abundance throughout the study.

2. Methods

2.1. Development of length-based age-structured mark-recapture (LAMR) model

The model uses a variety of estimated parameters, inputs and functions to predict catch length frequencies (Table 1). Variables and parameters used in the model are listed in Table 2. The model proceeds through the following steps: (1) predict initial age structure of the population and allocate among GTGs; (2) progress fish of each year-class and GTG through a year and calculate catches during capture events; (3) transition of each year-class and GTG between years; and (4) calculate catch length frequencies by summing catches across GTGs and ages at each capture event. Fish are assumed to recruit into the population at the beginning of the year (January 1). Model code and files necessary to evaluate the rainbow trout case study below are provided online (<https://github.com/bvanpoor/LAMR.git>).

Table 1

Length-based age-structured mark-recapture (LAMR) model. Symbols are defined in Table 2.

Length Assignment	
T1.1	$\bar{L}_{y,a,t}$: see van Poorten et al. (2012)
T1.2	$\sigma_{y,a,t} = \bar{L}_{y,a,t} cv_l$
T1.3	$L(i)_{y,a,t} = \bar{L}_{y,a,t} \left[1 + \frac{(2i-1+1)}{I-1} \right]$
Initial states	
T1.4	$U_j = \mu_R e^{\epsilon_j - 0.5\sigma_R^2}$
T1.5	$p(i \bar{L}_{y,a,t}, \sigma_{y,a,t}) = \frac{1}{\sigma_{y,a,t} \sqrt{2\pi}} \int_{L(i)_{y,a,t} - \frac{w}{2}}^{L(i)_{y,a,t} + \frac{w}{2}} e^{-\frac{(L(i)_{y,a,t} - \bar{L}_{y,a,t})^2}{2\sigma_{y,a,t}^2}} dL(i)_{y,a,t}$
T1.6	$U_{y=1,a,t=1,i} = U_{j=A-a+1} p(i \bar{L}_{y=1,a,t=1}, \sigma_{y=1,a,t=1}) e^{-M(a)}$
T1.7	$R_{y=1,a,t=1,i} = 0$
T1.8	$U_{y,a=1,t=1,i} = U_{j=y+A} p(i \bar{L}_{y=1,a,t=1}, \sigma_{y=1,a,t=1})$
T1.9	$R_{y,a=1,t=1,i} = 0$
Predicted catch	
T1.10	$\hat{u}_{y,a,t,G,i} = U_{y,a,t,i} \frac{s(L)_{GqG} E_i}{Z(L)_i} (1 - e^{-Z(L)_i})$
T1.11	$\hat{r}_{y,a,t,G,i} = R_{y,a,t,i} \frac{s(L)_{GqG} E_i}{Z(L)_i} (1 - e^{-Z(L)_i})$
T1.12	$Z(L)_i = \sum_G (s(L)_{GqG} E_i) + M\Delta t$
Gear selectivity	
T1.13	$s_{G,g} = \left(\frac{1}{1 - \gamma_G} \right) \left(\frac{1 - \gamma_G}{\gamma_G} \right)^{\gamma_G} \frac{\exp[\alpha_G \gamma_G (\beta_G - 1)(g)_{yc,a}]}{1 + \exp[\alpha_G (\beta_G - 1)(g)_{yc,a}]}$ G = 1,2
T1.14	$s(L)_G = \frac{1}{1 + \exp[-\alpha_G (\beta_G - L)]}$ G = 3
State dynamics	
T1.15	$U_{y,a,t,i} = [U_{y,a,t-1,i} - \sum_G (\hat{u}_{y,a,t-1,G,i} (p_{u-R} + p_{u-N}))] e^{-M\Delta t}$
T1.16	$R_{y,a,t,i} = [R_{y,a,t-1,i} - \sum_G (\hat{r}_{y,a,t-1,G,i} \cdot p_{r-N}) + \sum_G (\hat{u}_{y,a,t-1,G,i} \cdot p_{u-R})] e^{-M\Delta t}$
End-of-year transitions	
T1.17	$U_{y,a,t=1,i} = (U_{y-1,a-1,t=36,i} + R_{y-1,a-1,t=36,i}) e^{-M\Delta t}$
T1.18	$R_{y,a,t,i} = 0$

The LAMR model is conditioned on sampling intensity so the number of nets (or other suitable unit of sampling effort) at each capture occasion is required. The mean growth rate of each population over time is also required for which any growth function can be used. We used the Walters and Essington (2010) general bioenergetics model modified to account for varying growth rates in different years (van Poorten et al., 2012). While growth and abundance can be estimated simultaneously by adding likelihood components, we chose to estimate growth parameters separately and treat them as fixed in the abundance model. We explore model sensitivity to this separation approach below.

Mean length of fish, $\bar{L}_{y,a,t}$, at each age (a) in each year (y) and within-year time-step (t) is based on the model presented in van Poorten et al. (2012; Eq. T1.1). The standard deviation around the mean length ($\sigma_{y,a,t}$) is calculated by multiplying the mean length by an estimated coefficient of variation (Eq. T1.2). The actual lengths of fish in each GTG (i) at any year, age, time-step combination ($L(i)_{y,a,t}$) is provided in Eq. T1.3.

The population is initialized by predicting recruitment to each year-class and allocating it among growth-type groups. Annual recruitment of each year-class (U_j) is predicted by multiplying a mean recruitment (μ_R) by an annual residual (ϵ_j) that is exponentiated and bias corrected (Eq. T1.4; Maunder and Deriso, 2003). Recruits in each year class are normally distributed among GTGs according to their growth relative to the mean growth rate (Eq. T1.5). The abundance of unmarked fish in each year-class in the first year is predicted based on the proportion of initial recruits allocated among GTGs surviving from the age-at-recruitment to the beginning of the study according to a constant instantaneous mortality rate (Eq. T1.6). It is assumed there are no marked fish in the first year (Eq. T1.7). Likewise, fish recruiting in each subsequent year are normally distributed among GTGs to predict initial

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