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 $L(i)_{y,a,t} = \bar{L}_{y,a,t} \left[1 + \frac{(2i - I + 1)}{I - 1} \right]$

Initial states

T1.4 $U_j = \mu_R e^{\varepsilon_j - 0.5\sigma_R^2}$

T1.5 $p(i|\bar{L}_{y,a,t}, \sigma_{y,a,t}) = \frac{1}{\sigma_{y,a,t}\sqrt{2\pi}} \int_{L(i)_{y,a,t} - \frac{w}{2}}^{L(i)_{y,a,t} + \frac{w}{2}} e^{-\frac{(L(i)_{y,a,t} - \bar{L}_{y,a,t})}{2\sigma_{y,a,t}^2}} dL(i)_{y,a,t}$

T1.6 $U_{y=1,a,t=1,i} = U_{j=A-a+1} p(i|\bar{L}_{y,a,t=1}, \sigma_{y,a,t=1}) e^{-M(a)}$

T1.7 $R_{y=1,a,t=1,i} = 0$

T1.8 $U_{y,a=1,t=1,i} = U_{j=y+A} p(i|\bar{L}_{y,a,t=1}, \sigma_{y,a,t=1})$

T1.9 $R_{y,a=1,t=1,i} = 0$

Predicted catch

T1.10 $\hat{u}_{y,a,t,G,i} = U_{y,a,t,i} \frac{s(L)_G q_G E_t}{Z(L)_t} (1 - e^{Z(L)_t})$

T1.11 $\hat{r}_{y,a,t,G,i} = R_{y,a,t,i} \frac{s(L)_G q_G E_t}{Z(L)_t} (1 - e^{Z(L)_t})$

T1.12 $Z(L)_t = \sum_G (s(L)_G q_G E_t) + M\Delta t$

Gear selectivity

T1.13 $s_{G,g} = \left(\frac{1}{1 - \gamma_G} \right) \left(\frac{1 - \gamma_G}{\gamma_G} \right)^{\gamma_G} \frac{\exp[\alpha_G \gamma_G (\beta_G - l(g)_{yc,a})]}{1 + \exp[\alpha_G(\beta_G - l(g)_{yc,a})]}$ 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

Table 2
Definition of symbols and equations.

Symbol	Value	Description
Indices		
y	{1,2,…,Y}	Sampling year index ($Y = 8$)
a	{0,1,…,A}	Age in years ($A = 6$)
j	{1,2,…,J}	Year-class ($J = Y + A - 1$)
t	{1,2,…,T}	10-day annual time step index ($T = 36$)
G	{1,2,3}	Gear-type index for large fyke nets (1), small fyke-nets (2) and gill nets (3)
i	{1,2,…,I}	Growth-type-group ($I = 100$)
l	{1,2,…,L}	Length-bin ($L = 50$)
Constants		
w	10 mm	Length-bin width
Δt	1/T	Time-step as a proportion of year
Model parameters		
q_G	+ +	Catchability of gear G (ha net^{-1})
$\alpha_G, \beta_G, \gamma_G$	+ +	Selectivity parameters of gear G
cv_l	+ +	Coefficient of variation in length-at-age
μ_R	+ +	Mean recruitment density (ha^{-1})
σ_R	+ +	Standard deviation in recruitment
ε_Y	+ +	Annual recruitment deviation
M	0.65/+ +	Instantaneous natural mortality rate (yr^{-1}; fixed in simulation-evaluation; estimated for case study)
H_y	varied by year[a]	Mass-normalized net rate of mass acquisition
m	0.44	Mass-normalized rate of mass loss through catabolism
d	0.66	anabolism to mass scalar
n	1.0	catabolism to mass scalar
Q_c	3.35	Q10 parameter for consumption
Q_m	1.98	Q10 parameter for metabolism
Derived variables		
$\overline{L}_{y,a,t}$		Mean length-at-age of fish (estimated in van Poorten et al., 2012)
$p(i\|L_{y,a,t}, \sigma_{y,a,t})$		Probability of being in GTG-i given $L_{y,a,t}$ and $\sigma_{y,a,t}$
U_j		Recruitment of fish to year-class j
$\sigma_{y,a,t}$		Standard deviation in length-at-age
$s(L)_G$		Selectivity of fish length-L to gear-G
State variables		
$L(i)_{y,a,t}$		Length-at-age, -year and -time step for GTG-i
$U_{y,a,t,i}$		Density of unmarked fish in year y, age a, time-step t and GTG i
$R_{y,a,t,i}$		Density of marked fish of year y, age a, time-step t and GTG i
$\hat{u}_{y,a,t,G,i}$		Estimated unmarked catch in year y, age a, time-step t in gear G in GTG i
$\hat{r}_{y,a,t,G,i}$		Estimated recaptured catch in year y, age a, time-step t in gear G in GTG i
Observations		
$E_{y,t,G}$		Sampling intensity at time-t for gear G
$u_{(L)y,t,G,l}$		Unmarked length-based catch in year y, time-step t in gear G in length bin l
$r_{(L)y,t,G,l}$		Recaptured length-based catch in year y, time-step t in gear G in length bin l
$u_{(A)y,t,G,a,l}$		Unmarked length-at-age-based catch in year y, time-step t in gear G in length bin l
$r_{(A)y,t,G,a,l}$		Recaptured length-at-age-based catch in year y, time-step t in gear G in length bin l
Observed fates of catch		
$p_{u\text{-}R}$		Unmarked catch subsequently marked and released as a proportion of all unmarked catch
$p_{u\text{-}r}$		Unmarked catch subsequently released unmarked as a proportion of all unmarked catch
$p_{u\text{-}N}$		Unmarked catch subsequently not released as a proportion of all unmarked catch
$p_{r\text{-}N}$		Recaptured catch subsequently not released as a proportion of all recaptured catch
$pa_{y,t,G}$		Proportion of catch in year y, time step t, gear G that was aged

[a] see van Poorten et al. (2012).

unmarked abundance of subsequent year-classes (Eqs. T1.8, T1.9).

The predicted population propagates through each year as follows: the subpopulations of marked and unmarked fish in each GTG are captured in each time-step, t, with a probability defined by their size and the fishing mortality rate on that GTG. Catch of unmarked and marked fish in each time-step is calculated using the Baranov equation (Quinn and Deriso, 1999; Eqs. T1.10 and T1.11, respectively) based on total mortality calculated for the mean size of the GTG (Eq. T1.12). Selectivity is set as dome-shaped for the mark-recapture gear (Eq. T1.13; Thompson, 1994) and asymptotic for the depletion gear (Eq. T1.14), but other functions may be used. Predicted catch is then subject to three fates. The first is unmarked catch that are removed from the unmarked subpopulation, predicted by multiplying the observed proportion of unmarked captured fish that were either marked or died in sampling by the predicted unmarked catch of each GTG. The second fate is unmarked catch that are moved to the marked population, predicted by multiplying the observed proportion of unmarked captured fish that were subsequently marked by the predicted unmarked catch of each GTG. Finally, the marked catch that died due to sampling is predicted by multiplying the observed proportion of recaptured fish that died in sampling by the predicted marked catch of each GTG. These fish are removed from the marked subpopulation. The remaining fish in each subpopulation in each time step are subject to mortality (Eqs. T1.15 and T1.16) to predict numbers at the start of the next time step. At the end of each year, fish are assumed to lose their mark and return to the unmarked population, a conservative assumption that can be waived if necessary. Therefore, the abundance of unmarked fish in the next year ($y + 1$) and age ($a + 1$) is the sum of unmarked and marked fish in each GTG at the end of the previous year, and the abundance of marked fish at the same time is reset to zero (Eqs. T1.17 and T1.18, respectively). If fish are assumed to retain marks across years, Eq. T1.17 would have unmarked fish in the next year would simply be the sum of unmarked fish in each age-class and GTG in the previous year; likewise, marked fish in each age-class and GTG would be advanced by a year.

To compare predicted catches of fish across GTGs with observed catch in length-bins, or length-bins and age-classes, the catches of unmarked and marked fish in each sampling occasion, gear-type and GTG (Eqs. T1.10 and T1.11) are summed across year-classes and GTGs that have predicted lengths within each length-bin. The fit of model-predicted length-based catch of marked and unmarked fish is evaluated by assuming that numbers captured varied as Poisson log-likelihoods (Eqs. T3.3 and T3.4; Table 3), which is appropriate for capture-recapture data and functionally equivalent to a binomial likelihood (e.g. Coggins et al., 2006; Korman et al., 2011). In cases where a proportion of captured fish in a gear are aged ($pa_{G,y,t}$), the catch can be separated into catch at length-l and catch at length-l and age-a, evaluated using separate log-likelihoods (Eqs. T3.5 and T3.6). The total log-likelihood is the sum of the log-likelihood for all marked and unmarked fish minus a normally distributed recruitment penalty (Maunder and Deriso, 2003; Eq. T3.2), given by Eq. T3.7. The total log-likelihood is maximized while varying parameters T3.1 to obtain estimates of annual recruitment, and length-based or numerical abundance at any point in the study.

2.2. Simulation evaluation of LAMR model and comparison with Jolly-Seber models

To evaluate the effect of alternative model assumptions and to determine the magnitude of error and bias in maximum likelihood parameter estimates using this method, the model was fit to data simulated using an individual-based model (IBM), which tracks the fate of all individual fish over time and demonstrates the effect of individual growth rates on probability of capture due to gear selectivity (Walters and Martell, 2004). Growth trajectories of each individual were determined by multiplying the mean growth trajectory (which varied by year) by a fixed deviation determined by the simulated coefficient of

Table 3
Likelihood function for fitting the LAMR model to catch-at-length observations.

Estimated parameters	
T3.1	$\theta = (q_G, \alpha_G, \beta_G, \gamma_G, cv_l, \mu_R, \sigma_R, \varepsilon_j)$
Maximum log-likelihood components	
T3.2	$\ln P(\varepsilon_j \mid \sigma_R) = \sum_y \ln\left(\sigma_R + \dfrac{\varepsilon_j^2}{2\sigma_R^2}\right)$
T3.3	$\ln L(u_l \mid \theta) = \sum_G \sum_y \sum_t \sum_l - \widehat{m}_{y,t,G,l}(1 - pa_{G,y,t}) + \widehat{m}_{(L)y,t,G,l}\ln[\widehat{m}_{y,t,G,l}(1 - pa_{G,y,t})].$
T3.4	$\ln L(m_l \mid \theta) = \sum_G \sum_y \sum_t \sum_l - \widehat{r}_{y,t,G,l}(1 - pa_{G,y,t}) + r_{(L)y,t,G,l}\ln[\widehat{r}_{G,y,t,l}(1 - pa_{G,y,t})]$
T3.5	$\ln L(u_a \mid \theta) = \sum_G \sum_y \sum_t \sum_l - \widehat{m}_{y,t,G,a,l}pa_{G,y,t} + m_{(A)y,t,G,a,l}\ln[\widehat{m}_{y,t,G,a,l}pa_{G,y,t}]$
T3.6	$\ln L(m_a \mid \theta) = \sum_G \sum_y \sum_t \sum_l - \widehat{r}_{y,t,G,a,l}pa_{G,y,t} + r_{(A)y,t,G,a,l}\ln[\widehat{r}_{y,t,G,a,l}pa_{G,y,t}].$
Log-likelihood	
T3.7	$\ell = \ln L(u_l \mid \theta) + \ln L(m_l \mid \theta) + \ln L(u_a \mid \theta) + \ln L(m_a \mid \theta) - \ln P(\varepsilon \mid \sigma_R)$

Table 4
Parameters simulated and estimated in LAMR model.

Parameter	Simulation Scenario		
	Transformation	Mean Value	Coefficient of Variation
H	None	7.0/9.0	–
m	None	0.6	–
d	None	0.7	–
n	None	1.0	–
Q_c	None	2.5	–
Q_m	None	6.0	–
M	None	0.65	–
q_1	Natural Log	0.05	0.10
α_1	Natural Log	0.06	0.10
β_1	Natural Log	75	0.05
γ_1	Logistic	0.08	0.05
q_2	Natural Log	0.025	0.10
α_2	Natural Log	0.075	0.10
β_2	Natural Log	85	0.05
cv_l	Natural Log	0.15/0.30	0.05
μ_R	Natural Log	400	0.05
σ_R	Constant	0.6	–

Note: Simulated parameters were randomly chosen from normal distributions with transformed means and coefficients of variation shown. Subscript *1* refers to mark-recapture gear (such as fyke nets); subscript *2* refers to depletion gear (such as gill nets).

variation in length at age. Therefore, growth for all fish may vary over years, as in the LAMR model, but there were persistent differences in individual growth from the mean trajectory. The structure and assumptions used in the IBM were exactly the same as in the LAMR estimation model, except individuals were tracked rather than year-classes grouped by GTG. Unless specified otherwise, populations were simulated over six consecutive years; number of individuals simulated from each year-class was randomly determined by drawing from a lognormal distribution with mean of 400 fish per year (Table 4). Untransformed parameters for each simulation were drawn from a normal distribution. Mean and coefficients of variation for each simulated parameter over simulation-evaluation trials are found in Table 4. The simulation-evaluation procedure was repeated over 100 Monte-Carlo simulation trials and proportional error was calculated from each trial. Data generated did not include any aged sub-samples of catch, so represent a worst-case scenario because the estimation model was only fit to catch-at-length data.

The simulation model was used for various evaluations of the LAMR model. Indices and parameters varied across the different evaluations are shown in Table 5. First, proportional errors in population abundance estimated using the LAMR model were compared with estimates from the POPAN (Schwarz and Arnason, 1996) Jolly-Seber model. Mark-recapture data for the POPAN model were generated using the IBM assuming all fish were individually identified over a six-year simulation with seven sampling occasions each year and six units of fishing effort per occasion (Table 6). Fish were sampled with replacement and capture gear exhibited an asymptotic vulnerability. Parameters are shown in Table 4, with low net consumption rate ($H = 7.0$) and low variation in length-at-age ($cv_l = 0.15$). Abundance was estimated in POPAN assuming survival probabilities proportional to the time-interval between observations, analogous to the constant mortality rate in the simulation model. The POPAN model assumed capture probability either varied with length at initial capture or with the actual size-based vulnerability used to generate the data, with vulnerability based on length at initial capture. The corresponding LAMR population estimates were based on bulk-marking of fish (fish were either unmarked or recaptured). In each simulation-evaluation, the same data were used in the POPAN and the LAMR model (though POPAN evaluated individual mark data whereas LAMR evaluated bulk marks), so true comparisons could be made.

The second evaluation of the LAMR model examined how population life history and sampling intensity affected model performance. Data were generated using the IBM assuming two gear-types. The first gear used for mark-recapture (G_1), was assumed to be non-destructive so fish could be returned to the population and marked if appropriate (mark-recapture sampling), whereas the second gear (G_2) was for depleting the population (removal sampling). This second gear improves information on population abundance and coincides with the sampling of fish on lakes in our field study (see Field Data Collection, below), but is not necessary in a mark-recapture experiment. Data were simulated using two series of fishing efforts (Sampling scenario 1 or 2; Table 6), and sampling duration (*i.e.* years of data; short: 3 yrs (= 0.5 A), long: 6 yrs (= A)). Selectivity to the mark-recapture gear was defined by mean parameters that resulted in 50% selectivity at 65 mm, full selectivity at 113 mm and declined to 75% selectivity by 190 mm. Selectivity of the depletion gear was defined by mean parameters resulting in 50% selectivity at 82 mm, and full selectivity at 205 mm. Growth parameters were also systematically varied (low: $L_{age-3} = 100$ and $L_{age-5} = 130$; high: $L_{age-3} = 300$ and $L_{age-5} = 400$ by varying net consumption rate, *H*, from the Walters and Essington (2010) bioenergetics model to either 7.0 or 9.0), as was variation around length-at-age (low: $cv_l = 0.15$; high: $cv_l = 0.3$). The sampled population was assumed to have a maximum age, *A*, of 6 years.

The next model evaluation examined the ability of the LAMR model to estimate annual recruitment across species of different longevity. Length-based catch data were generated assuming six years of sampling a population with low effort (Sampling scenario 1: Table 6), sampling a

Table 5

Indices and parameters varied across each of the simulation evaluations of the LAMR model.

Evaluation	Cormack-Jolly-Seber	Life history and sampling intensity	Longevity	Growth	Recruitment variation
Purpose	Compare abundance predictions between LAMR and POPAN	Evaluate parameter error given different sampling intensity, study length, growth rates and coefficient of variation in length at age	Evaluate how parameter error is affected by species longevity	Evaluate how errors in growth parameters affect error in estimated parameters	Evaluate year-class recruitment estimates when one early recruitment year has anomalous year-class strength
Gear 1 effort ($E_{Y=1}$)	6	{3, 6}	3	3	3
Gear 2 effort ($E_{Y=2}$)[a]	NA	{10, 20}	10	10	10
Maximum age (A)	6	6	{6, 12}	6	30
Years of sampling (Y)	8	{4, 8}	8	8	8
Net consumption (H)	7	{7.7, 7.0, 6.3}	7	7	7
net metabolism (m)	0.6	{0.54, 0.60, 0.66}	0.6	0.6	0.6
Coefficient of variation – length (cv_l)	0.15	{0.02, 0.15}	0.15	0.15	0.15

[a] Gear 2 was only applied the last three sampling events each year.

Table 6

Effort used in each year in data simulations for evaluation of model performance.

Day of Year	Jolly-Seber evaluation	Sampling scenario 1		Sampling scenario 2		Smearing evaluation	
	Mark-recapture effort	Mark-recapture effort	Removal effort	Mark-recapture effort	Removal effort	Mark-recapture effort	Removal effort
150	6	3	0	6	0	6	0
170	6	3	0	6	0	6	0
200	6	3	0	6	0	6	0
230	6	3	0	6	0	6	0
260	6	3	0	6	0	6	0
270	6	3	10	6	20	6	20
280	6	3	10	6	20	6	20
290	6	3	10	6	20	6	20

Note: Fyke net effort is in net-nights per hectare and gill net effort is in panel-nights per hectare. Three evaluation-types are shown: The first is effort used to generate individual capture histories to compare a POPAN Jolly-Seber model with LAMR. The second demonstrated the value of additional sampling effort by contrasting a low and high effort scenario. The third evaluated the potential for smearing in long-lived, slow growing populations. Effort data are repeated over either 6 or 12 years.

Table 7

Total annual sampling effort (fyke net net-nights or gill net panel-nights) across all eight study lakes from 2001 to 2008 using fyke nets, small fyke nets and standard gill net configurations.

Lake	Surface Area (ha)	Sample Year							
		2001	2002	2003	2004	2005	2006	2007	2008
Fyke Net Effort									
Cheryl	12.4	0	10	16	3	25	114	30	24
Cath	2.7	0	0	0	0	0	122	124	124
Dad`s	8.4	0	7	15	0	32	26	24	28
Meghan	3.8	0	0	0	0	0	20	18	16
Mom`s	6.1	0	8	15	0	16	18	28	24
Nestor	7.5	0	10	16	0	20	40	30	32
Moose Pasture	5.9	0	47	16	0	25	34	34	32
Wilderness	10.9	0	12	16	0	0	58	50	50
Small Fyke Net Effort									
Cheryl	12.4	0	4	5	0	11	75	33	30
Cath	2.7	0	0	0	0	0	9	11	11
Dad`s	8.4	0	4	10	0	16	25	24	26
Meghan	3.8	0	0	0	0	0	21	15	14
Mom`s	6.1	0	3	6	0	6	18	24	21
Nestor	7.5	0	3	6	0	10	32	27	28
Moose Pasture	5.9	0	15	5	0	12	34	26	36
Wilderness	10.9	0	4	4	0	0	38	34	34
Gill Net Effort									
Cheryl	12.4	1154	0	0	0	0	1476	426	426
Cath	2.7	0	0	0	0	0	108	108	108
Dad`s	8.4	0	0	0	0	0	285	285	285
Meghan	3.8	0	0	0	0	0	208	138	138
Mom`s	6.1	400	0	0	0	0	222	222	222
Nestor	7.5	8	800	0	0	0	384	279	279
Moose Pasture	5.9	0	0	0	0	0	201	201	201
Wilderness	10.9	552	0	0	0	0	568	393	393
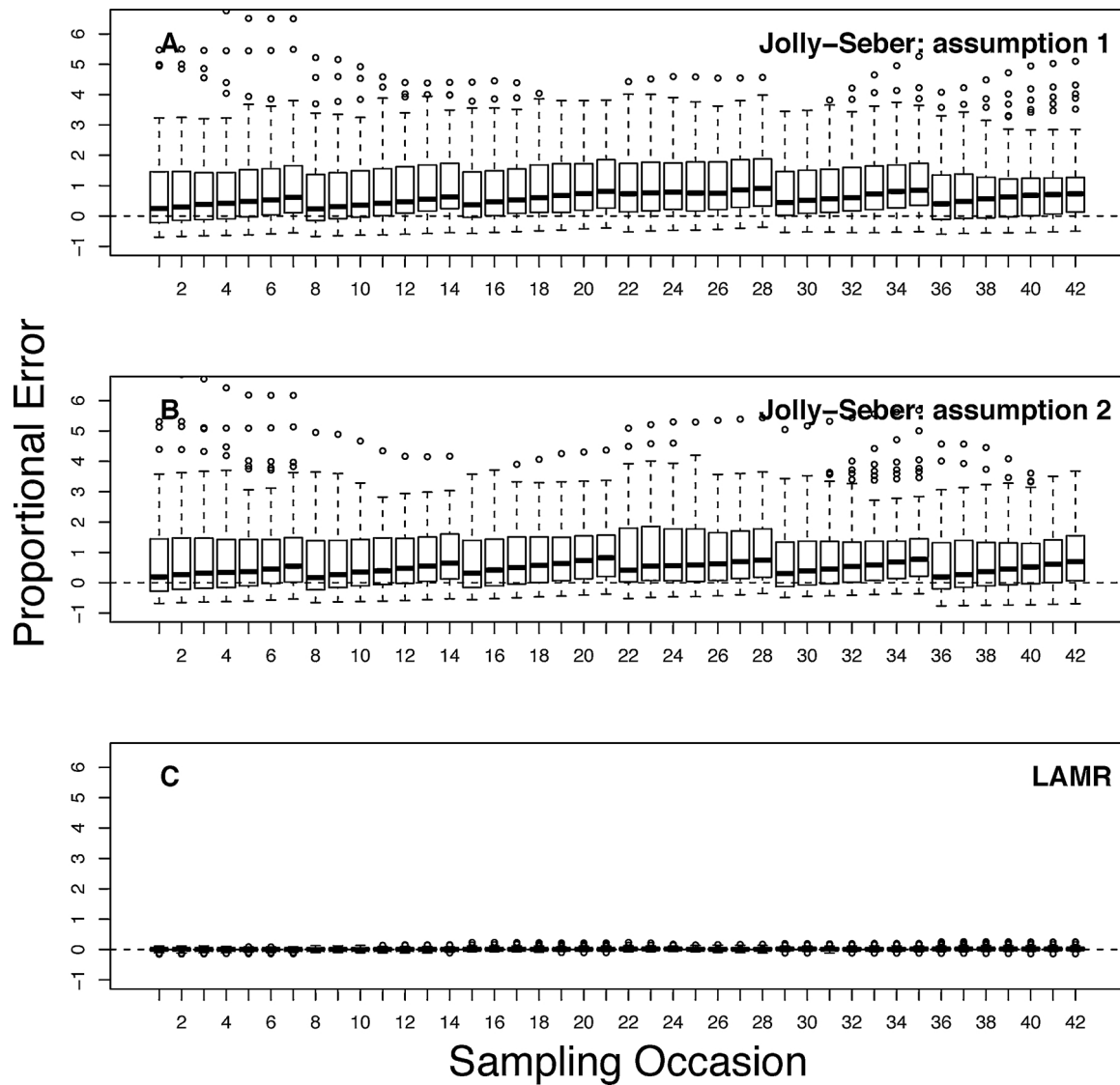
Fig. 1. Box and whisker plot of proportional error [(Estimate – True)/True] between 100 generated and estimated population abundance estimates at each sampling occasion. Panel A shows estimated abundance using the POPAN Jolly-Seber model assuming capture probability is a function of size at marking; Panel B was shows estimated abundance using the POPAN Jolly-Seber model assuming capture probability is a function of the true vulnerability to the capture gear at the time of marking; Panel C shows estimated abundance estimated using the LAMR model.

population with low growth ($H = 7.0$; Table 4) and low coefficient of variation in length. The two scenarios in this evaluation examined proportional error in parameter estimates when the life-span of the population being studied is either equal to or double the number of sampling years (i.e. six or 12 years).

The LAMR length-based model is conditioned on fixed growth parameters, which we assume are known with certainty. To evaluate the potential for growth parameter misspecification to introduce bias into parameter estimates, we generated data using the IBM as above with sampling effort based on Sampling scenario 1 (Table 6) and estimated them using LAMR with either the net consumption rate (H) or net metabolic rate (m) set 10% higher or lower than the simulated population.

The final model evaluation examined the ability to accurately estimate to anomalously high recruitment in older year-classes. Length-based methods are often prone to difficulties distinguishing one strong versus multiple weak recruitment events in successive years, a phenomenon known as 'smearing' (Pitcher, 2002; Walters and Martell, 2004). In early year-classes that have high overlap in size-structure at the start of the experiment, the model assumes a series of intermediate

recruitment years rather than a single high recruitment year. This is especially true in slow-growing species. To evaluate this, we used the IBM to generate catch data from a long-lived population ($A = 30$) with low growth ($H = 2.0$, $m = 0.8$) and high coefficient of variation in length ($cv_l = 0.3$). Sampling was conducted using Sampling scenario 1 in Table 6. Recruitment anomalies were generated using a standard deviation of 0.6 except in year-class 7, which experienced recruitment 10-times the mean recruitment across all other years. The estimation model was then used to estimate parameters to determine whether smearing of recruitment estimates occurs for long-lived species with low growth.

2.3. Case study: rainbow trout populations

Field data were collected from a series of eight lakes in south-central British Columbia, Canada on the Bonaparte Plateau, which we collectively refer to as the Bonaparte Lakes. Each lake contains populations of rainbow trout (which we refer to as trout herein), which co-occur with northern pikeminnow (*Ptychocheilus oregonensis*). All lakes are within five kilometers of one another on a low-relief landscape at similar

Table 8
Median proportional error (with 2.5% and 97.5% percentiles in parentheses) for all scenarios exploring model sensitivity to sampling program and life history of the studied population.

Scenario settings				Estimated parameter performance				
Effort	Study length	Growth rate	cv_l	Mark-recapture gear selectivity	Depletion gear selectivity	cv_l	Early recruitment	Late recruitment
$G_1 = 3$; $G_2 = 10$	3 years	Low	Low	0.01 (−0.77, 3.57)	−0.05 (−1.00, 4.30)	0.02 (−0.01, 0.07)	0.03 (−0.33, 1.07)	0.02 (−0.15, 0.23)
			High	0.00 (−0.63, 1.40)	0.00 (−0.54, > 100)	0.00 (−0.04, 0.04)	0.05 (−0.49, 1.92)	0.01 (−0.18, 0.31)
		High	Low	0.02 (−0.83, 5.10)	−0.01 (−1.00, 3.43)	0.02 (−0.01, 0.06)	0.02 (−0.43, 1.01)	0.00 (0.20, 0.33)
			High	0.00 (−0.97, 3.40)	0.02 (−1.00, > 100)	0.00 (−0.03, 0.04)	0.05 (−0.53, 2.00)	0.01 (−0.19, 3.00)
	6 years	Low	Low	−0.01 (−0.36, 0.45)	−0.01 (−0.53, 1.65)	0.00 (−0.02, 0.03)	0.04 (−0.50, 2.00)	0.00 (−0.14, 0.21)
			High	−0.01 (−0.55, 1.23)	−0.05 (−1.00, 6.65)	0.02 (0.00, 0.06)	0.03 (−0.32, 0.78)	0.01 (−0.12, 0.18)
		High	Low	−0.01 (−1.00, 3.87)	−0.02 (−1.00, > 100)	0.03 (0.00, 0.05)	0.03 (−0.35, 1.10)	0.01 (−0.14, 0.02)
			High	0.00 (−0.55, 1.26)	0.07 (−0.72, > 100)	0.01 (−0.02, 0.03)	0.04 (−0.52, 1.54)	0.01 (−0.17, 0.21)
$G_1 = 6$; $G_2 = 20$	3 years	Low	Low	−0.01 (0.66, 1.99)	−0.02 (−1.00, 5.57)	0.02 (−0.01, 0.05)	0.05 (−0.32, 1.00)	0.02 (−0.10, 0.14)
			High	−0.02 (−0.55, 0.86)	0.00 (−0.70, 4.10)	0.00 (−0.03, 0.02)	0.02 (−0.50, 2.17)	0.02 (−0.12, 0.19)
		High	Low	0.01 (−0.88, 3.03)	0.00 (−1.00, > 100)	0.03 (0.01, 0.06)	0.01 (−0.36, 0.94)	0.01 (−0.10, 0.16)
			High	0.00 (−0.90, 1.45)	0.01 (−1.00, > 100)	0.01 (−0.02, 0.03)	0.04 (−0.53, 2.00)	0.01 (−0.11, 0.18)
	6 years	Low	Low	−0.01 (−0.55, 1.23)	−0.05 (−1.00, 6.65)	0.02 (0.00, 0.06)	0.03 (−0.32, 0.78)	0.01 (−0.12, 0.18)
			High	−0.01 (−0.31, 0.48)	−0.01 (−0.68, 1.23)	0.00 (−0.02, 0.02)	0.04 (−0.50, 1.55)	0.01 (−0.10, 0.16)
		High	Low	−0.01 (−0.90, 1.82)	−0.01 (−1.00, 29.31)	0.02 (0.00, 0.05)	0.02 (−0.30, 0.84)	0.01 (−0.07, 0.10)
			High	0.00 (−0.47, 0.82)	0.04 (−0.58, > 100)	0.00 (−0.02, 0.03)	0.02 (−0.05, 1.64)	0.01 (−0.09, 0.15)

Note: Medians were calculated from 100 estimates generated by fitting the LAMR model to data generated with an individual-based model. Parameter groupings comprise of: fyke-net (G1) selectivity (includes catchability and selectivity parameters); gill net (G2) selectivity (includes catchability and selectivity parameters); coefficient of variation in length-at-age; and recruitment for year-classes recruiting to the gear prior to study onset (early recruitment) and after study onset (late recruitment). Bias estimates of each parameter within a grouping were pooled before bias was calculated.

elevation and experience similar environmental conditions and growing seasons (Taylor, 2006); however population densities, sampling intensities and sampling duration all vary across lakes and within lakes over the course of the study. Rainbow trout in the Bonaparte populations exhibit slow growth for the species (van Poorten et al., 2012). All lakes are foot access only and quite remote. A private fishing lodge targeting rainbow trout exists in the middle of the study area, but fishing pressure on trout from the lodge on the study lakes is usually quite low and external fishing pressure is non-existent. Fishing mortality in all lakes except that caused by sampling is assumed negligible.

Bonaparte populations were sampled using a combination of fyke nets and gill nets from 2001 to 2008, although not all lakes were sampled in all years. Fyke nets are classified as small (60 cm hoop diameter) or large (90 cm hoop diameter) nets, each with a unique size-selectivity. Gill nets consisted of a standardized combination of panels with stretched mesh ranging from 13 to 89 mm (Post et al., 1999; Askey et al., 2007). Annual sampling effort on each lake in each year is given in Table 7. Sampling consisted of a combination of year-specific mark-recapture experiments and occasional removal netting, where all fish captured were measured and removed from the population to manipulate densities. Removal sampling occasions targeting trout occurred in Wilderness Lake in 2001 and in Nestor Lake in 2002 and again in all lakes from 2006 to 2008 (Table 7). Scales were collected during each depletion sampling occasion to assess age from a subset of captured fish (van Poorten et al., 2012). During mark-recapture sampling, fish captured in fyke nets were usually marked with a spaghetti tag and/or given a fin clip, measured and released. Minimum lengths for tagging varied over the study depending on tag size, but typical minimum sizes were 120 mm. Captured fish below the minimum tagging size were given a fin clip unique to each capture year. Overwinter tag loss was assumed high, and fin clips were unreliable after one year, so marks were assumed to last one year; fish recaptured after the first year were assumed to be unmarked in the data and the model. This combination of multiple sampling gears, the combination of marking and depleting techniques and the loss of marks after each year creates an analysis problem which is not readily treated using standard Jolly-Seber mark-recapture techniques.

Trout size data were summarized using 60 length bins with width of 10 mm. The date of recruitment was set at January 1 each year, corresponding to age-0.5, since they typically rear in streams in their first summer. One hundred GTGs were used for each year-class. Note there are no established rules for deciding on the most appropriate number of GTGs. We evaluated several options and settled on 100 as it was enough to ensure simulated length-frequencies were not 'choppy' (i.e. there were no length-bins that were between GTGs) and additional GTGs did not change estimated parameters. Any number of GTGs could be used, but too many does not improve estimates and significantly slows down estimation time.

All populations were evaluated simultaneously, allowing for some parameters to be shared across populations. The model assumed catchability and selectivity for each of the three fishing gears (small fyke nets, large fyke nets and gill nets) were constant across years and lakes. Variation in size-at-age (cv_l) was also shared across lakes. Selectivity of the two fyke nets was always assumed to be dome-shaped, following Eq. T1.13; selectivity of gill nets was assumed to be asymptotic (Askey et al., 2007), following Eq. T1.14. Mean and standard deviation in recruitment anomalies (σ_R) were estimated separately for each lake. We estimated a single recruitment deviation for all year-classes older than one-third of the maximum age of trout at the start of the study. All parameters were bounded to be above zero by log-transformation, except γ_G, which was bounded to be between 0 and 1 by logit-transformation, and the annual recruitment residual, which was untransformed and bounded to be between −10 and 10. Natural mortality rate was estimated using a normal prior probability distribution with mean of 0.58 and 10% coefficient of variation.
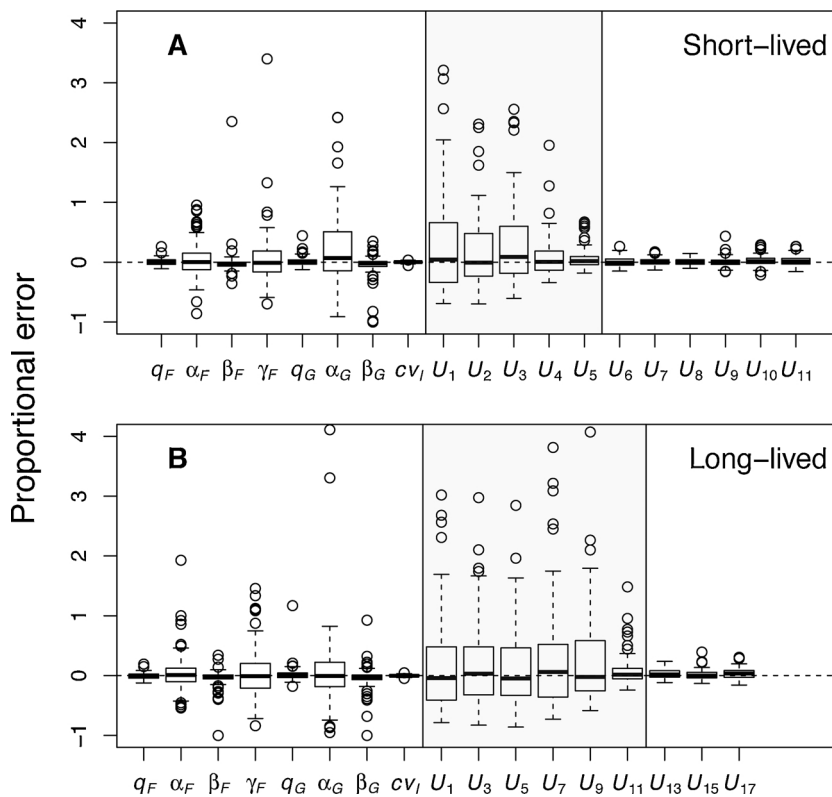
Fig. 2. Box and whisker plot of proportional error between 100 generated and estimated parameters used in the LAMR model. The plot represents a slow-growing population with low variation in length-at-age, sampled with high effort for a short period (6 years). Panel A: short-lived population (A = 6); Panel B: long-lived population (A = 12). Recruitment estimates for alternating years are shown in Panel B. U_j refers to the recruitment estimate for year-class-j, where the age of a year-class in a particular year of sampling is determined as $j = A - a + y$ (e.g. U_{11} will be age-1 in the sixth sampling year if $A = 6$, but age-2 in the first sampling year if $A = 12$). Early recruitment year-classes are within the shaded region.

3. Results

Comparisons of the POPAN Jolly-Seber model with the LAMR model demonstrated the risk of ignoring growth variation in mark-recapture abundance estimates when there is size-selective fishing (Fig. 1). Population estimates assuming capture probability varied with initial length were positively biased and bias generally increased throughout each year due to small fish becoming increasingly catchable (higher vulnerability: Fig. 1A). Median bias across all sampling events was 0.58. When the POPAN model assumed capture probability varied with the true vulnerability at first capture, a similar pattern was seen (Fig. 1B). Median bias across all sampling events in this scenario was 0.47. Equivalent estimates based on the LAMR model were slightly positive biased and relatively precise with no discernible pattern within or across years; median bias across all sampling events was 0.01 (Fig. 1C).

Median proportional absolute error was less than 0.07 for all parameters across all simulated scenarios of fishing effort, study length and population growth characteristics when using the LAMR model (Table 8). Increased fishing effort generally led to improvements in parameter estimates because of increased sample size and recapture rates, especially in the range of proportional error within a parameter grouping. Longer study length marginally improved parameter estimates. Selectivity parameters were better estimated when growth rate was low and cv was low; most other parameters were insensitive to growth. Estimates of parameters associated with selectivity and catchability of the two gears were the most difficult to estimate, particularly for the depletion gear, which was only used for three occasions within each year (Table 6). The coefficient of variation in length-at-age (cv_l) was well defined across all scenarios, even in instances where actual cv_l was quite high, leading to substantial overlap in size-distributions of adjacent age-classes. Within recruitment estimates, bias was consistently greater for year-classes that recruited prior to the beginning of the study (referred to henceforth as early recruitment) than for year-classes that recruited within the years of the study (late recruitment; Table 8, Fig. 2).

The maximum age of the simulated population being studied did not

appreciably affect the estimates of any parameters using the LAMR model. The exception was that in an older-lived population, there are more early recruited year-classes for which the range of proportional error is higher than late recruited year-classes (Fig. 2). All parameters had minimal bias, although early recruitment estimates often had a slight positive median bias across simulations and extreme cases can extend beyond twice the value of the true estimate.

Mis-specifying growth parameters, specifically net consumption rate (H) and net metabolic rate (m) led to under- or overestimation of length-at-age (Fig. 3) in the LAMR model, which had a corresponding effect in the predicted mode of length frequencies of age-classes in the model and parameter estimates. When consumption in the estimation model was mis-specified by +10%, annual recruitment estimates of late year-classes showed positive bias (Fig. 3B). When consumption in the estimation model was mis-specified by −10%, early year-classes had a positive bias in recruitment whereas late year-classes had neutral or negative bias (Fig. 3C). A change in the net metabolic rate had little effect on length-at-age for young fish, but progressively influenced the predicted length-at-age of older fish (early recruitment; Fig. 3E). Accordingly, mis-specifying net metabolic rate had no impact on recruitment estimates of late recruited year-classes (Fig. 3E; F).

Simulated data from the IBM were used to evaluate the potential for the LAMR model to smear recruitment estimates in slow growing, long-lived species. The estimation model was able to reasonably estimate most year-classes, with 95% confidence intervals overlapping the true recruitment, except for the year-classes 6–8, where the year class with the disproportionately high simulated recruitment (year-class 7) was underestimated and the adjacent year-classes were overestimated (Fig. 4). These estimated year-classes also showed higher uncertainty in recruitment estimates than many other year-classes because the estimate of recruitment variability across years was underestimated. This confirms that for early recruits in long-lived, slow growing species, year-by-year recruitment estimates are somewhat of a running average of true recruitment across year-classes because the assumption of annual recruitment being normally distributed is violated.

Mean recruitment estimates for trout varied across lakes, however
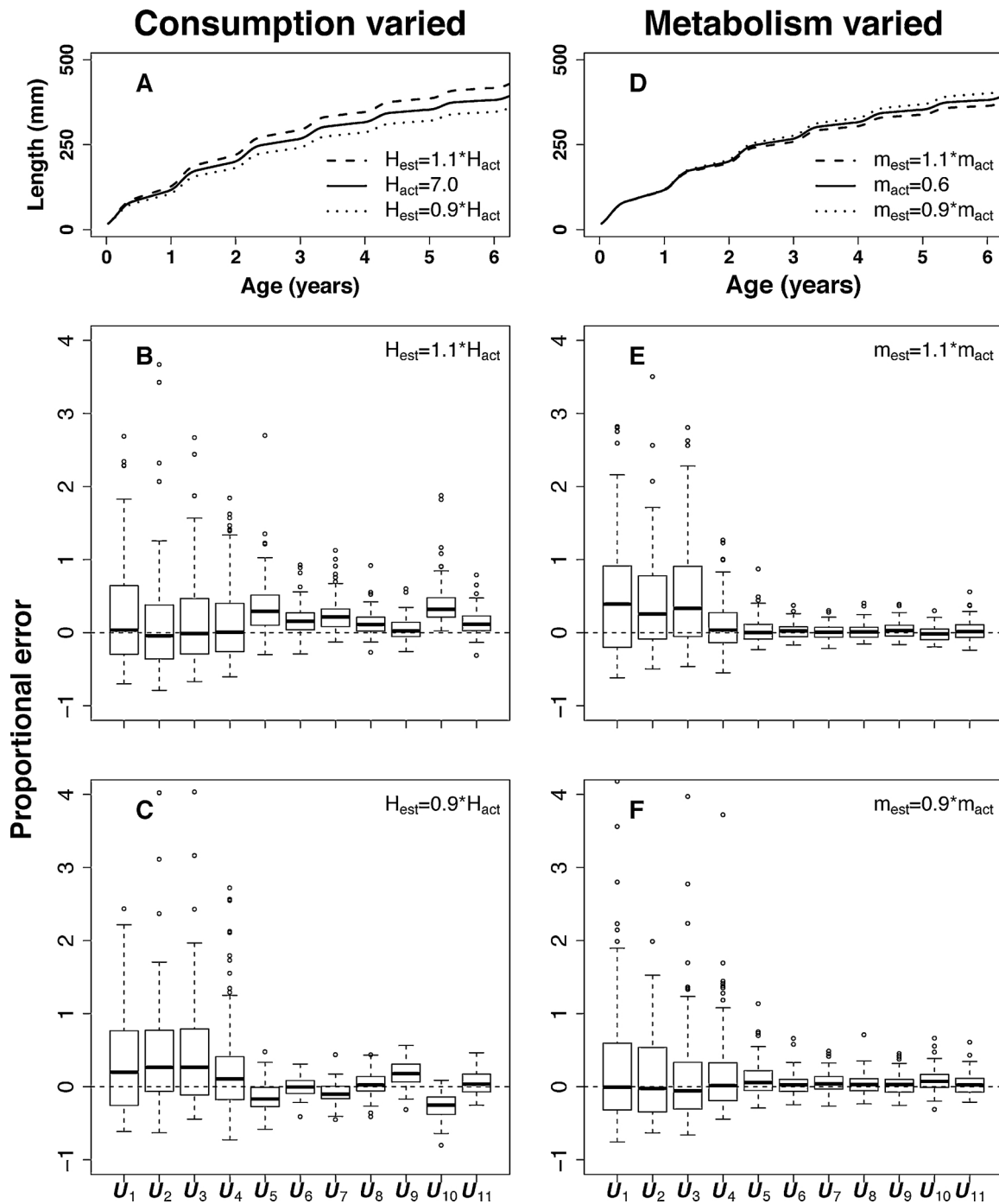
Fig. 3. Box and whisker plots of proportional error demonstrating the effect of incorrectly specifying consumption (left panels) and metabolism (right panels) parameters used for the growth submodel as inputs in the LAMR model. Panel A shows the effect of a ± 10% change of consumption on lifetime growth; Panels B–C respectively show the proportional error in recruitment estimates when consumption is incorrectly specified as +10% (panel B) or −10% (panel C) the true value. Panel D shows the effect of a ± 10% change in metabolism on lifetime growth; Panels E–F respectively show the proportional error in recruitment estimates when metabolism is incorrectly specified as +10% (panel E) or −10% (panel F) the true value. H_{est} and H_{act} refer to estimated and actual H (net consumption rate); m_{est} and m_{act} refer to estimated and actual m (net metabolic rate); U_j refers to the recruitment estimate for year-class j.

all lakes showed occasional strong year-classes (Fig. 5). High mean recruitment in Wilderness and Nestor lakes, which were depleted of adults in 2001 and 2002, respectively, had low subsequent recruitment thereafter, although Nestor had two poor year-classes leading up to the depletion. Abundance of trout in most lakes declined over the course of the study, but total abundance was quite variable due to high levels of recruitment relative to the overall abundance (Fig. 6). In lakes with poor catches (Cath and Meghan lakes), individual abundance estimates are most uncertain.

4. Discussion

Mark-recapture studies over protracted periods of time are typically analysed using open population models such as variations on the Jolly-Seber model (Seber, 1982), which can estimate recruitment into the population of interest through birth or immigration, as well as abundance and survival (Pine et al., 2003; Schwarz and Seber, 1999). However, none of these models explicitly allow for growth and consequent individual changes in capture probabilities to be included,
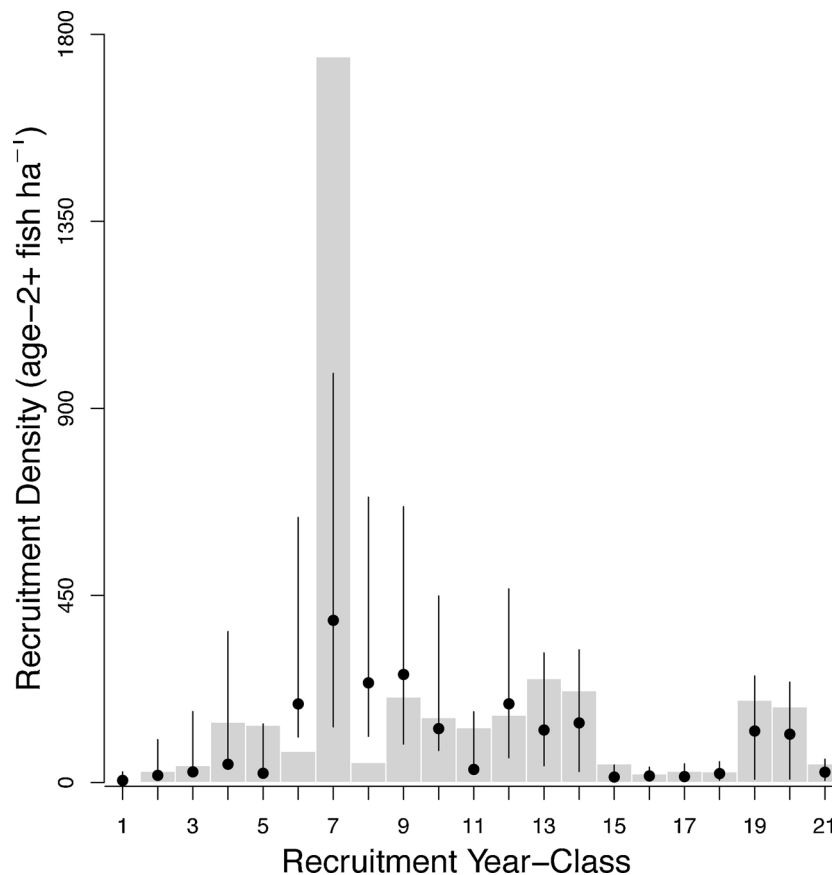
Fig. 4. Simulated (grey bars) and estimated (points) recruitment density associated with sampling effort for a long-lived, slow growing population with one large recruitment anomaly in year-class 5. Vertical bars represent 95% confidence intervals.

thereby potentially leading to biases in recruitment and abundance estimates. We have demonstrated that with standard Jolly-Seber models, a bias does exist, even when the exact form of gear selectivity is known (which in practice would rarely happen). A key problem with Jolly-Seber models is predicting the length of marked individuals in sampling occasions where they are not captured, so that only the length at initial capture can be used as a proxy for individual capture probability (Schwarz and Seber, 1999). The LAMR model assumes a persistent deviation of all fish from the mean population growth trajectory (in the form of growth-type groups), consistent with inter-individual observations (e.g. Biro et al., 2014), allowing differences in capture probability between marked and unmarked fish to be estimated. In fact, our population estimates based on the POPAN model indicate the median error at each sampling occasion is approximately +75% across sampling occasions for our specific scenarios. The extent of bias will depend on a number of factors, especially the growth rates of animals in the population, however estimating how this will impact abundance estimates is beyond scope of this paper. The LAMR model presented here is effective at estimating recruitment and abundance when individual variation in growth caused marked and unmarked individuals to have fundamentally distinct and time-varying capture probabilities.

Estimating animal abundance is often conducted using one of several approaches: mark-recapture methods; catch-effort methods; or depletion methods. Estimating abundance and recruitment of small populations can often be carried out only using mark-recapture because removal of animals will disturb the study population or is not possible due to conservation concerns. Protracted studies would either rely on open population estimates such as the Jolly-Seber model or the Robust Design model, which combines open and closed methods to address unequal catchability over time (Kendall et al., 1995; Pollock, 1982; Schwarz and Seber, 1999). As shown here, any estimates based on

protracted sampling will be biased due to the unequal capture probabilities of marked and unmarked animals in situations where the capture gear is size-selective because fish exhibit indeterminate growth. In harvested populations with high abundance, it is often more common to estimate an abundance time-series through the use of catch-effort models, where the changes in catch-per-unit effort (CPUE) is attributed to observed removals or harvest effort (Hilborn and Walters, 1992; Schwarz and Seber, 1999). Harvest in commercially fished populations is often relatively constant or increasing over time so there is no chance for the population to partially recover. This results in 'one-way trip' data (Walters and Martell, 2004), where it is difficult to separate population productivity from abundance (Hilborn and Walters, 1992) because the population index (CPUE) can be either from a productive, highly catchable population, or an unproductive, largely invulnerable population. Incorporating mark-recapture into catch-effort models allows for substantial information gain (Polacheck et al., 2006) in situations where reducing harvest rates is not possible. The LAMR model can be used in either context: small populations where marking is size-selective and large populations where mark-recapture could be incorporated to improve parameter estimation (Cadigan, 2016). Mark-recapture data carry substantial information on capture probability that could greatly enhance the ability to estimate abundance in data poor studies (Besbeas et al., 2002; Polacheck et al., 2006). We see the LAMR model as a substantial addition to the analysis of both mark-recapture and time-series data.

Our results highlight the difficulty in estimating the true magnitude of recruitment variation when an occasional high recruitment event occurs prior to the onset of data collection. This is common in length-based methods because of high overlap in size-at-age for older year-classes (Pitcher, 2002). This may also be due to an underestimate of the standard deviation of recruitment residuals (σ_R), as is common with the
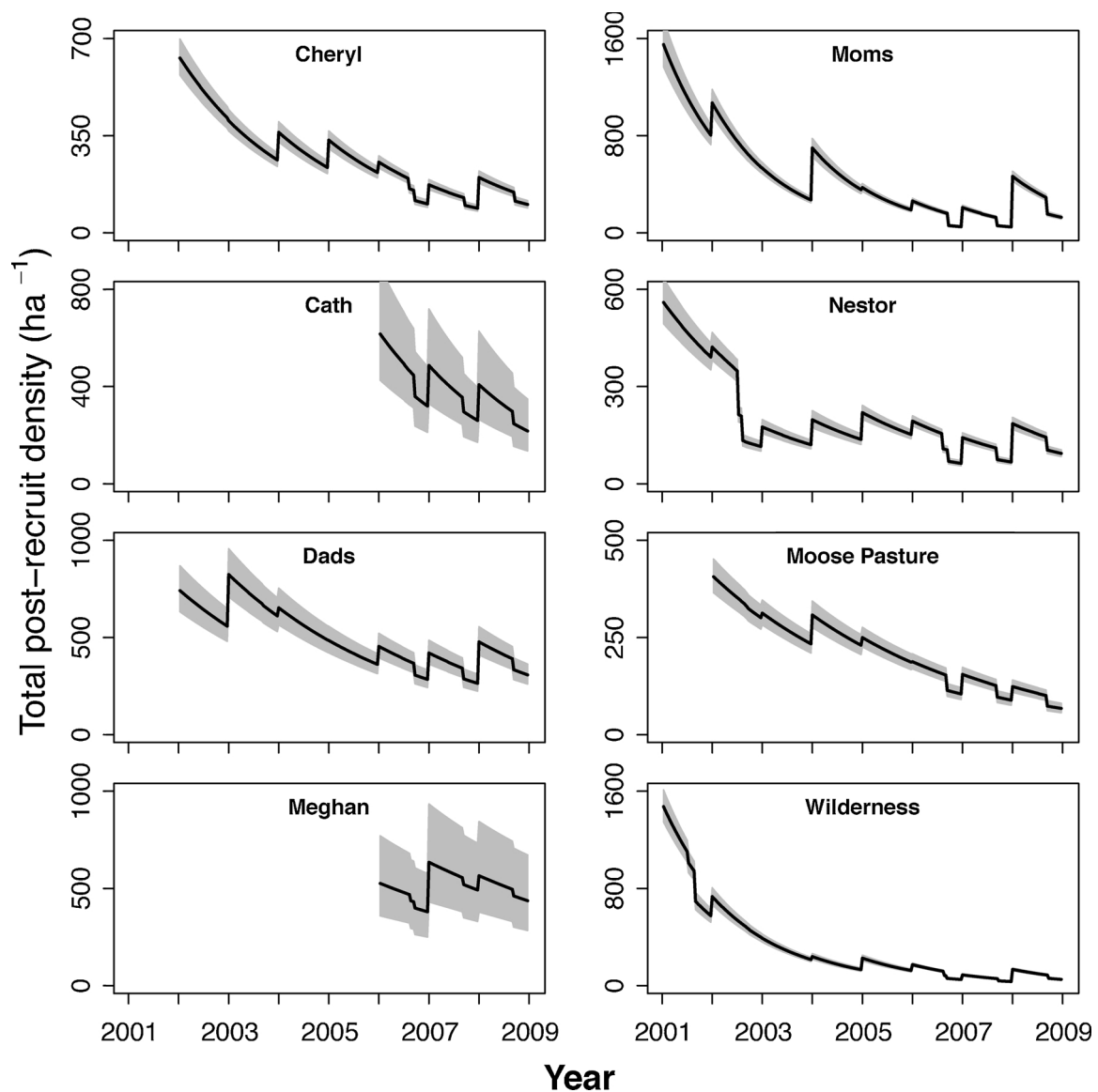
Fig. 5. Estimated rainbow trout recruitment densities. Vertical error bars represent 95% confidence limits; year-class recruitment estimates of approximately zero recruitment are shown without error. Confidence limits for small recruitment densities are not visible because of y-axis scaling. Note different y-axis scaling among panels.

penalized likelihood used here (Maunder and Deriso, 2003). To correct the underestimation of σ_R, Maunder and Deriso (2003) suggest using a Bayesian approach, which could also be incorporated here by setting annual recruitment estimates as random effects with associated hyperparameters for mean and standard deviation characterizing annual recruitment (similar to the penalty function used here). Alternately, in situations where the full recruitment history is not of critical importance or where sufficient age-samples are not available, we recommend pooling all older age-classes as demonstrated with the Bonaparte rainbow trout populations.

There are several key assumptions of this model which will be met in experimental settings, where fishing mortality is limited or closely monitored, but may not be met in other situations. The first is that fishing mortality is known or absent. Obviously this is difficult to know in many situations and special attention will need to be paid to this assumption in future applications of this model. Populations with fishing will likely require additional data to account for this otherwise unexplained mortality. The model is also conditioned on sampling effort, which may be known in research settings (where the researcher is the one doing the fishing), but may be highly uncertain in situations

where commercial fisheries are collecting data. Finally, natural mortality rate is fixed, which will strongly influence final abundance estimates (Clark, 1999). All of these assumptions may limit the applicability of the model to larger-scale experiments with high uncertainty in these rates. Although not examined here, the use of informative prior probability distributions around these rates based on external information may help provide useful information to facilitate the use of this model in those situations.

The LAMR model is useful for removing bias due to variation in size-based capture probability, especially due to sub-year growth, but its use is not appropriate in all situations. LAMR and the bioenergetics model that it relies on are both data intensive. The bioenergetics model either requires fish to be aged or a relatively large number of recaptures within the year from individuals that span the length distribution of the population (Walters and Essington, 2010). LAMR may be paired with another growth model, but sub-year length-at-age predictions are necessary, which will certainly require detailed information on growth. However, we have shown the resulting bias associated with ignoring size-based changes to capture probability and suggest this extra data requirement is a cost of accuracy in abundance estimates. Obviously, if
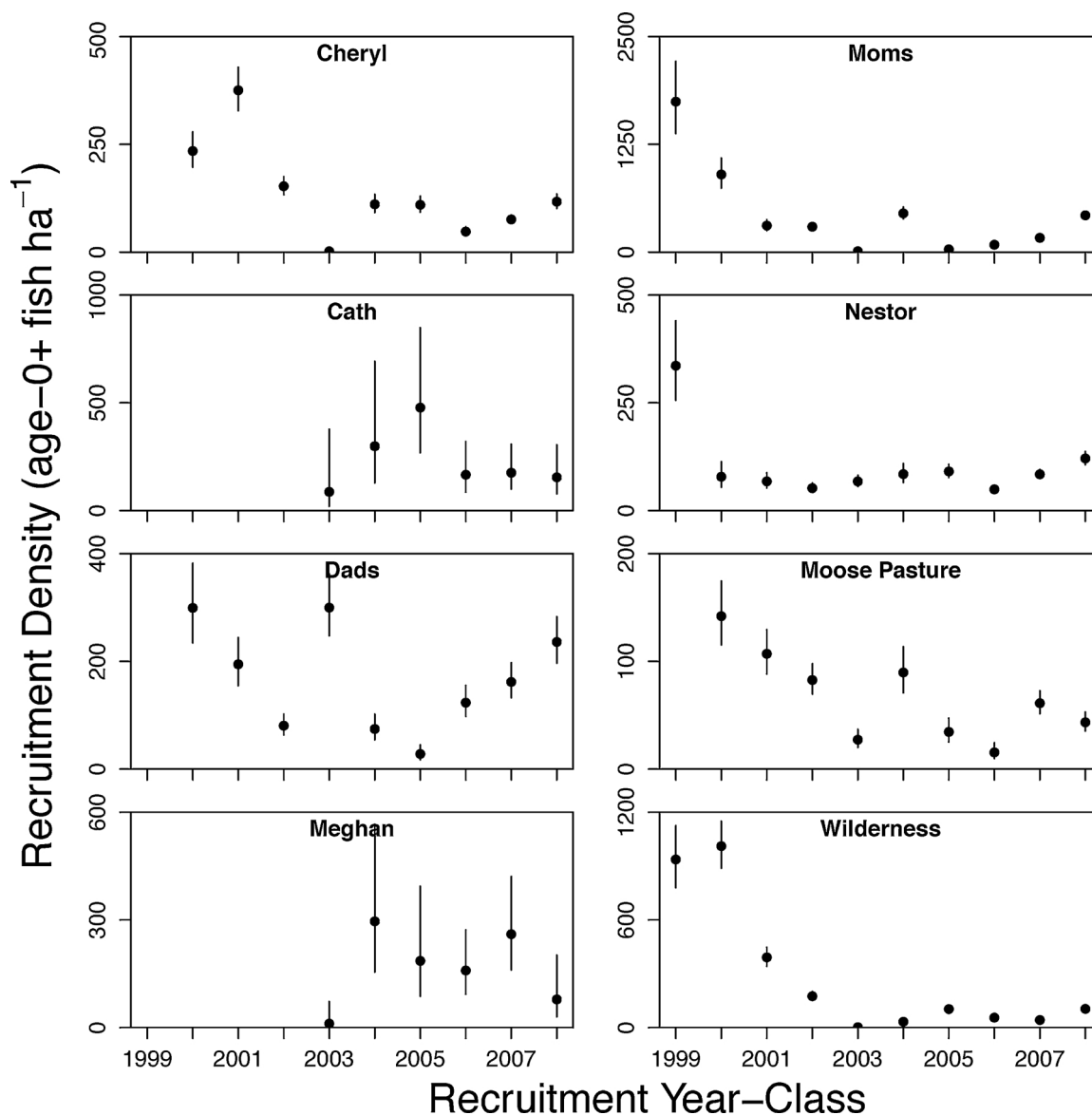
Fig. 6. Time-series of rainbow trout population density for all recruited age-classes. Solid lines are mean numbers at time and shaded areas are 95% confidence limits. X-axis ticks represent January 1 of the indicated year.

fish are resighted using methods that are not size-selective (e.g. PIT tags or similar remote detection; Barbour et al., 2013), LAMR will not be necessary, although could still be used by presuming selectivity is equal across lengths. However, resighting studies do not require recapture of fish, which has additional benefits, such as evaluating growth, allowing inference of consumption and broader ecosystem impacts and threats (van Poorten and Walters, 2016).

The LAMR model estimates a time-series of size- and age-based abundance, which can be useful for determining various size-based rates, such as consumption and competition. Preliminary evaluations demonstrated that both total density and size-based density measures such as effective density, measured as the squared length across all fish in a population (Post et al., 1999), are unbiased and relatively precise (van Poorten, 2012). By estimating both mean population body growth and therefore age-specific consumption (van Poorten et al., 2012) as well as total age- and size-specific abundance it is possible to obtain an accurate estimate of total effect of the population on the resources through consumption or competition. These rates have ecosystem-wide

implications and are particularly important when attempting to determine the implications of changes of management to one or more species on the ecosystem (Carpenter and Kitchell, 1996).

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