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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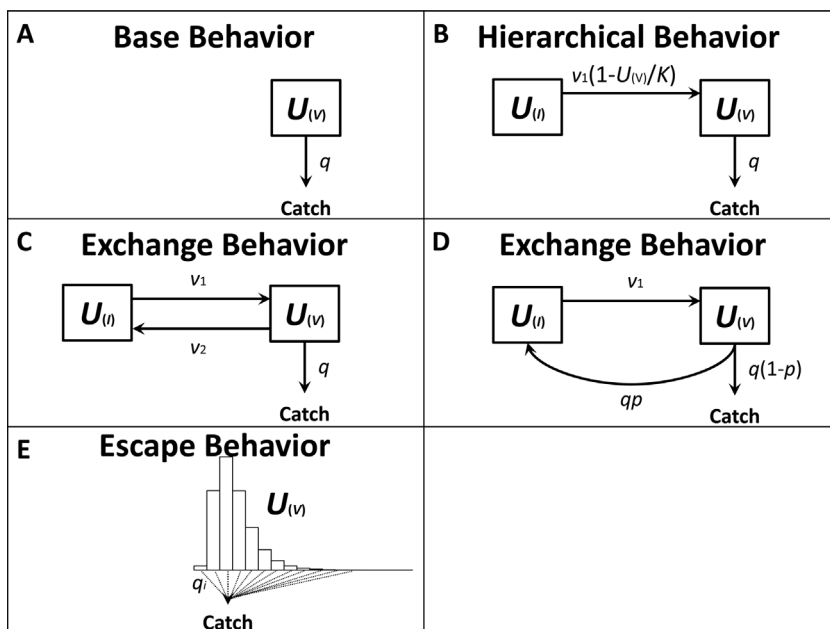 E-mail address: brett.vanpoorten@gov.bc.ca (B.T. van Poorten).

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

Table 1

Behavioral simulation models used to generate removal catch data across five fishing events assuming marks are randomly assigned to fish. Note a time-index of j+ refers to an intermediate step after capture and before movement between states; j+1 refers to numbers in the next step prior to capture.

Model 1 (base)

T1.1	$\Theta = (N_0, q)$	
T1.2	$U_{(V)i,1} = 1 - M_{(V)i,1}$	$M_{(V)i,1} \sim Bern\left(\frac{M_0}{N_0}\right)$
T1.3	$u_{i,j} \sim Bern(U_{(V)i,j}\,q)$	$m_{i,j} \sim Bern(M_{(V)i,j}\,q)$
T1.4	$U_{(V)i,j+1} = U_{(V)i,j} - u_{i,j}$	$M_{(V)i,j+1} = M_{(V)i,j} - m_{i,j}$

Model 2 (Hierarchy)

T1.5	$\Theta = (N_0, q, v_1, K)$	
T1.6	$U_{(V)i,0} \sim Bern\left(\frac{K}{N_0}\right);\; U_{(I)i,0} = 1 - U_{(I)i,0}$	
T1.7	$U_{(V)i,1} = 1 - M_{(V)i,1};\; U_{(I)i,1} = 1 - M_{(I)i,1}$	$M_{(V)i,1} \sim Bern\left(U_{(V)i,0}\frac{M_0}{N_0}\right);\; M_{(I)i,1} \sim Bern\left(U_{(I)i,0}\frac{M_0}{N_0}\right)$
T1.8	$u_{i,j} \sim Bern(U_{(V)i,j}\,q)$	$m_{i,j} \sim Bern(M_{(V)i,j}\,q)$
T1.9	$U_{(V)i,j+} = M_{(V)i,1} - u_{i,j}$	$M_{(V)i,j+} = M_{(V)i,1} - m_{i,j}$
T1.10	$\delta_{u,i,j+} \sim Bern\left(v_1 U_{(I)i,j+}\left[1 - \frac{\sum_{i=1}^{I}\left(U_{(V)i,j+} + M_{(V)i,j+}\right)}{K}\right]\right)$	$\delta_{m,i,j+} \sim Bern\left(v_1 M_{(I)i,j+}\left[1 - \frac{\sum_{i=1}^{I}\left(U_{(V)i,j+} + M_{(V)i,j+}\right)}{K}\right]\right)$
T1.11	$U_{(V)i,j+1} = U_{(V)i,j+} + \delta_{u,i,j+}$	$M_{(V)i,j+1} = M_{(V)i,j+} + \delta_{m,i,j+}$
T1.12	$U_{(I)i,j+1} = U_{(I)i,j} - \delta_{u,i,j+}$	$M_{(I)i,j+1} = M_{(I)i,j} - \delta_{m,i,j+}$

Model 3 (Exchange)

T1.13	$\Theta = (N_0, q, v_1, v_2)$	
T1.14	$U_{(V)i,0} \sim Bern\left(\frac{v_1}{v_1 + v_2}\right);\; U_{(I)i,0} = 1 - U_{(I)i,0}$	
T1.15	$U_{(V)i,1} = 1 - M_{(V)i,1};\; U_{(I)i,1} = 1 - M_{(I)i,1}$	$M_{(V)i,1} \sim Bern\left(U_{(V)i,0}\frac{M_0}{N_0}\right);\; M_{(I)i,1} \sim Bern\left(U_{(I)i,0}\frac{M_0}{N_0}\right)$
T1.16	$u_{i,j} \sim Bern(U_{(V)i,j}\,q)$	$m_{i,j} \sim Bern(M_{(V)i,j}\,q)$
T1.17	$U_{(V)i,j+} = U_{(V)i,j} - u_{i,j}$	$M_{(V)i,j+} = M_{(V)i,j} - m_{i,j}$
T1.18	$\delta_{u,i,j+} \sim Bern(v_1 U_{(I)i,j+})$	$\delta_{m,i,j+} \sim Bern(v_1 M_{(I)i,j+})$
T1.19	$\gamma_{u,i,j+} \sim Bern(v_2 U_{(V)i,j+})$	$\gamma_{m,i,j+} \sim Bern(v_2 M_{(V)i,j+})$
T1.20	$U_{(V)i+1,j} = U_{(V)i,j+} + \delta_{u,i,j+} - \gamma_{u,i,j+}$	$M_{(V)i,j+1} = M_{(V)i,j+} + \delta_{m,i,j+} - \gamma_{m,i,j+}$
T1.21	$U_{(I)i,j+1} = U_{(I)i,j} - \delta_{u,i,j+} + \gamma_{u,i,j+}$	$M_{(I)i,j+1} = M_{(I)i,j} - \delta_{m,i,j+} + \gamma_{m,i,j+}$

Model 4 (Escape)

T1.22	$\Theta = (N_0, q, p, v_1)$	
T1.23	$U_{(V)i,1} = 1 - M_{(V)i,1};\; U_{(I)i,1} = 0$	$M_{(V)i,1} \sim Bern\left(\frac{M_0}{N_0}\right);\; M_{(I)i,1} = 0$
T1.24	$u_{i,j} \sim Bern(U_{(V)i,j}\,q)$	$m_{i,j} \sim Bern(M_{(V)i,j}\,q)$
T1.25	$b_{u,i,j} \sim Bern(p \cdot u_{i,j})$	$b_{m,i,j} \sim Bern(p \cdot m_{i,j})$
T1.26	$U_{(V)i,j+} = U_{(V)i,j} - u_{i,j};\; U_{(I)i,j+} = U_{(I)i,j} + b_{u,i,j}$	$M_{(V)i,j+} = M_{(V)i,j} - m_{i,j};\; M_{(I)i,j+} = M_{(I)i,j} + b_{m,i,j}$
T1.27	$\delta_{u,i,j} \sim Bern(v_1 U_{(I)i,j+})$	$\delta_{m,i,j} \sim Bern(v_1 M_{(I)i,j+})$
T1.28	$U_{(V)i,j+1} = U_{(V)i,j+} + \delta_{u,i,j}$	$M_{(V)i,j+1} = M_{(V)i,j+} + \delta_{m,i,j}$
T1.29	$U_{(I)i,j+1} = U_{(I)i,j+} - \delta_{u,i,j}$	$M_{(I)i,j+1} = M_{(I)i,j+} - \delta_{m,i,j}$

Model 5 (Individual)

T1.30	$\Theta = (N_0, \mu_q, \sigma_q)$	
T1.31	$q_i \sim lnN(\mu_q, \sigma_q)$	
T1.32	$U_{(V)i,1} = 1 - M_{i,1}$	$M_{(V)i,1} \sim Bern\left(\frac{M_0}{N_0}\right)$
T1.33	$u_{i,j} \sim Bern(U_{(V)i,j}\,q_i)$	$m_{i,j} \sim Bern(M_{(V)i,j}\,q_i)$
T1.34	$U_{(V)i,j+1} = U_{(V)i,j} - u_{i,j}$	$M_{(V)i,j+1} = M_{(V)i,j} - m_{i,j}$

lognormal draws based on means and standard deviations listed in Table 3. Parameters were chosen to represent a small closed population with low capture probability and exchange rates that would permit some exchange of fish between reactive states within the space of a 5-day removal experiment. The sensitivity to the combination of small population with low capture probability is described in the online supplementary material. We present the status of each individual-i that may be previously unmarked ($U_{i,j} = 1$) or marked ($M_{i,j} = 1$) and subsequently captured in event-j. Subscripts (V) and (I) represent individuals in a state where they are vulnerable or invulnerable to capture, respectively. Therefore, the ith fish at event j may be in one of four states: unmarked and vulnerable ($U_{(V),i,j}$); unmarked and invulnerable ($U_{(I),i,j}$); marked and vulnerable ($M_{(V),i,j}$); or marked and invulnerable ($M_{(I),i,j}$). Catch of marked and unmarked fish are given as $u_j = 1$ and $m_j = 1$, respectively. Marked and unmarked fish were assumed to be functionally independent, but shared a common capture probability

and were affected by the same fishing effort. The number of fish caught in a removal event was a binomial process with probability of success equal to a capture probability (q) multiplied by the binary state of each individual. Note for the simulations where no fish were marked, $M_0 = 0$ and all marked equations drop out.

The first behavioral model (referred to as the Base model; Fig. 1A) was based on the Leslie removal model (Leslie and Davis, 1939) where capture probability was constant across time and individuals. All fish were vulnerable to capture and the probability of being marked was equal to the total proportion of fish that are marked (T1.2). Probability of a marked or unmarked fish being captured in any capture period was equal to the constant capture probability if it was available (i.e. if $M_{(V)i,j} = 1$ or $U_{(V)i,j} = 1$; T1.3). Marked and unmarked fish were removed from the population if they were captured (T1.4).

The second model (Hierarchy; Fig. 1B) assumed a social hierarchy such as territoriality, where some individuals defended more profitable

Table 2

Notation for the behavioral simulation models and estimation models. Parameters used to generate simulation model parameters are given in Table 3. The Models column indicates which of the simulation or estimation models utilized each of the model parameters and indicates differences in notation across simulation and estimation models for model variables. The symbol $++$ indicates parameters that are estimated.

Symbol	Value	Models		Description
		Simulation	Estimation	
Indices				
i	{1,2,...,N}			Individual fish
j	{1,2,...,T}			Removal event
Model parameters				
N_0	Table 3 $++$	all	all	Total abundance (includes unmarked and marked, vulnerable and invulnerable fish)
q	Table 3 $++$	1,2,3,4	all	Capture probability
q_1	$++$		2,3	Initial capture probability
a	$++$		3	Temporal rate of change in capture probability
β	$++$		5	Density dependent rate of change in capture probability
v_1	Table 3 $++$	2,3,4	4	Vulnerability exchange rates (d^{-1})
v_2	Table 3	3		
K	Table 3	2		Carrying capacity
p	Table 3 $++$	4	4	Proportion of catch that escapes gear
μq	Table 3	5		Mean capture probability across individuals
σq	Table 3	5		Standard deviation in capture probability across individuals
State variables				
$U_{(I)j}$		$U_{(I)j}$	$U_{(I)i,j}$	Invulnerable unmarked fish
$U_{(V)j}$		$U_{(V)j}$	$U_{(V)i,j}$	Vulnerable unmarked fish
$M_{(I)j}$		$M_{(I)j}$	$M_{(I)i,j}$	Invulnerable marked fish
$M_{(V)j}$		$M_{(V)j}$	$M_{(V)i,j}$	Vulnerable marked fish
$\hat{u}_j$				Estimated unmarked catch
$\hat{m}_j$				Estimated marked catch
$\delta_{u,i,j}$				Movement of unmarked fish into vulnerable state
$\delta_{m,i,j}$				Movement of marked fish into vulnerable state
$\gamma_{u,i,j}$				Movement of unmarked fish into invulnerable state
$\gamma_{m,i,j}$				Movement of marked fish into invulnerable state
Derived variables				
q_i				Individual-specific capture probability
q_j				Event-specific capture probability
$b_{u,i,j}$				Number of unmarked fish to escape capture
$b_{m,i,j}$				Number of marked fish to escape capture
Observations				
M_0				Number of fish marked prior to removal − set at 10% of N_0
u_j				Unmarked catch in event j
m_j				Marked catch in event j

habitats and excluded others from those areas. The number of socially dominant fish was determined by the carrying capacity K (where $K \leq N_0$). The probability of an individual initially being in the vulnerable state was given by K/N_0 (T1.6). The probability of a fish being marked was given as the proportion of all fish that were marked multiplied by whether that fish was vulnerable or invulnerable (T1.7). In this model, removal gear differentially favoured those profitable areas; therefore, only dominant, vulnerable fish were captured (T1.8). Once fish were removed from those areas, the probability of sub-dominant

fish moving into profitable habitats between each sampling period was given by a density-dependent rate (T1.10). Between capture events, vulnerable fish may have been removed through capture (T1.9); invulnerable fish may have changed to the vulnerable state (T1.10–T1.12).

The third model (Exchange; Fig. 1C) assumed exchange between vulnerable and invulnerable states due to shifts in behavior, habitat or activity. The probability of an individual initially being vulnerable was given by the equilibrium solution (T1.14; Walters and Juanes, 1993). The probability of individual fish being marked and unmarked was given as the proportion of all fish that were marked multiplied by whether that fish was vulnerable or invulnerable (T1.15). Probability of capture in each sampling period was equal to the constant capture probability (T1.16). Between capture events, vulnerable fish may have been removed through capture (T1.17) or became invulnerable (T1.19; T1.20); invulnerable fish may have become vulnerable (T1.18; T1.21).

The fourth behavioral model (Escape; Fig. 1D) assumed that all fish were vulnerable to the gear prior to the first removal event and marks were randomly assigned to fish with probability equal to the proportion of all fish marked (T1.23). Fish were captured with a constant capture probability (T1.24); captured fish may escape the gear with probability equal to a constant escape probability (p; T1.25). Between capture events, vulnerable fish may be removed through capture or become invulnerable after escaping the gear (T1.26); invulnerable fish may become vulnerable after recovering from the gear (T1.27-T1.29)

The final behavioral model (Individual; Fig. 1E) assumed all fish were vulnerable to capture, but capture probability was assumed lognormally distributed across individuals (T1.31). Note that the parameters chosen for the lognormal distribution give the capture probability a 95% probability of ranging from approximately 0.05-0.22. Marks were randomly assigned to fish with probability equal to the proportion of all fish marked (T1.32). Fish were captured with an individual capture probability that was invariant over time (T1.33), with captured fish removed from the population (T1.34).

2.2. Behaviors affecting marking and removal

The models described in Section 2.1 assumed that when marked fish were added to the population they were randomly mixed into the vulnerable and invulnerable populations. A more realistic scenario is that the behaviors that affect the removal process will also affect the marking process. Here we briefly describe how the behavioral models affect the initial abundance of marked and unmarked fish by the beginning of removal process.

Across all models, fish were assumed to be marked 10 days prior to the onset of removal. Whether each fish was marked was determined using a Bernoulli process based on the expected proportion of vulnerable fish that will be marked:

$$M_{i,1} \sim Bern\left(\frac{M_0}{\Sigma_{i=1}^{I} U_{(V)i,-10}}\right) \quad (1)$$

Marked fish were vulnerable (as were all fish) in the Base and Individual models, while marked fish in Eq. (1) were invulnerable to capture immediately after marking in the Hierarchy, Exchange and Escape models. Eq. (1) was modified in the Individual model to account for variation in capture probability: fish with higher capture probability were more likely to be marked. This is represented by

$$M_{i,1} \sim Bern\left(\frac{M_0}{\sum_{i=1}^{I} U_{(V)i,-10}}\frac{q_i}{\bar{q}}\right) \quad (2)$$

where $\bar{q}$ is the mean capture probability across all fish in the population.

Fish in the Hierarchical, Exchange and Escape behavioral models were removed from the vulnerable populations once marked. Fish may

Table 3
Back-transformed mean and standard deviation of lognormal sampling distributions used to generate parameters of the simulation models.

Model Parameter	Mean	Standard deviation
N_0	1000	100
q	0.1	0.005
v_1	0.05	0.001
v_2	0.08	0.0016
K	500	50
p	0.15	0.015
μq	0.1	0.005
σq	1.25	0.125

move into the vulnerable state based on the reduction of vulnerable fish during the 10-day period between marking and the initiation of removal. Whether a marked or unmarked fish moved into the vulnerable state followed the same rule as the behavioral models outlined above and are given in T1.10, T1.18, and T1.27.

2.3. Estimation models

Five removal models were used to estimate abundance across all behavioral models above. $M_1 = 0$ and all calculations involving marked fish drop out in situations where marked fish were not used.

The first estimation model (Base) assumed all fish were equally catchable. There were only two parameters in this model: N_0 and q (T4.1). Abundance of unmarked fish was calculated as the difference between the estimated total abundance and the known number of marks (T4.2). As with the base simulation model, capture probability was assumed constant (T4.3) and abundance declined due to removals (T4.4).

The second estimation model (Schnute 2) was based on Model 2 in Schnute (1983) and is designed to account for the initial capture of the most vulnerable fish. Three parameters were estimated in this model: N_0, q_1 and q (T4.5). Abundance of unmarked fish was calculated as the difference between estimated total abundance and the known number of marks (T4.6). In this model, capture probability in the first removal event was independent from all subsequent events (T4.7). Abundance of marked and unmarked fish declined due to removals (T4.8–T4.9).

The third estimation model (Schnute 3) is based on Model 3 in Schnute (1983) and is designed to account for the progressive removal of the most vulnerable fish. There were four parameters estimated in this model: N_0, q_1, q and a (T4.10). Abundance of marked and unmarked fish was calculated as the difference between estimated total abundance and the known number of marks (T4.11). Capture probability changed across sampling periods from q_1 to q at a rate of $(1-a^{j-1})$ (T4.12). Abundance of marked and unmarked fish declined due to removals (T4.13–T4.14).

The forth estimation model (Escape) is structured in the same way as the Escape behavioral simulation model where some fish escape the gear and are subsequently invulnerable. There are four parameters being estimated in this model: N_0, q, p and v_1 (T4.15). All fish started as equally vulnerable to capture and abundance of marked and unmarked vulnerable fish was calculated as the difference between estimated total abundance and the known number of marks (T4.16). Number of fish captured in each sampling period was based on a constant capture probability, but a proportion of fish caught by the fishing gear escape prior to being removed from the population (T4.17). Fish that escape were invulnerable to capture, but returned to the vulnerable group at a rate v_1 (T4.18–T4.19).

Table 4
Models used to estimate initial population abundance from removal and/or mark-recapture data.

Model 1 (base)		
T4.1	$\Theta = (N_0, q)$	
T4.2	$\hat{U}_1 = N_0 - M_0$	$\hat{M}_1 = M_0$
T4.3	$\hat{u}_j = \hat{U}_j q$	$\hat{m}_j = \hat{M}_j q$
T4.4	$\hat{U}_{j+1} = \hat{U}_j - u_j$	$\hat{M}_{j+1} = \hat{M}_j - m_j$
Model 2 (Schnute 2)		
T4.5	$\Theta = (N_0, q_1, q)$	$\Theta = (N_0, q_1, q)$
T4.6	$\hat{U}_1 = \hat{N}_0 - M_0$	$\hat{M}_1 = M_0$
T4.7	$q_j = \begin{cases} q_1, & j = 1 \\ q, & j = 2,...,T \end{cases}$	
T4.8	$\hat{u}_j = \hat{U}_j q_j$	$\hat{m}_j = \hat{M}_j q_j$
T4.9	$\hat{U}_{j+1} = \hat{U}_j - u_j$	$\hat{M}_{j+1} = \hat{M}_j - m_j$
Model 3 (Schnute 3)		
T4.10	$\Theta = (N_0, q_1, q, a)$	$\Theta = (N_0, q_1, q, a)$
T4.11	$\hat{U}_1 = \hat{N}_0 - M_0$	$\hat{M}_1 = M_0$
T4.12	$q_j = \begin{cases} q_1, & j = 1 \\ q_1 + (q - q_1)(1 - a^{j-1}), & j = 2,...,T \end{cases}$	
T4.13	$\hat{u}_j = \hat{U}_j q_j$	$\hat{m}_j = \hat{M}_j q_j$
T4.14	$\hat{U}_{j+1} = \hat{U}_j - u_j$	$\hat{M}_{j+1} = \hat{M}_j - m_j$
Model 4 (Escape)		
T4.15	$\Theta = (N_0, q, p, v_1)$	$\Theta = (N_0, q, p)$
T4.16	$\hat{U}_{(V)1} = \hat{N}_0 - M_0; \hat{U}_{(I)1} = 0$	$\hat{M}_{(V)1} = M_0; \hat{M}_{(I)1} = 0$
T4.17	$\hat{u}_j = \hat{U}_{(V)j} q(1 - p)$	$\widehat{m_i} = \hat{M}_{(V)j} q(1 - p)$
T4.18	$\hat{U}_{(V)j+1} = \hat{U}_{(V)j} + v_1 \hat{U}_{(I)j} - \hat{U}_{(V)j} q$	$\hat{M}_{(V)j+1} = \hat{M}_{(V)j} + v_1 \hat{M}_{(I)j} - \hat{M}_{(V)j} q$
T4.19	$\hat{U}_{(I)j+1} = (1 - v_1)\hat{U}_{(I)j} + \hat{U}_{(V)j} qp$	$\hat{M}_{(I)j+1} = (1 - v_1)\hat{M}_{(I)j} + \hat{M}_{(V)j} qp$
Model 5 (Density dependent)		
T4.20	$\Theta = (N_0, q, \beta)$	$\Theta = (N_0, q, \beta)$
T4.21	$\hat{U}_1 = \hat{N}_0 - M_0$	$\hat{M}_1 = M_0$
T4.22	$q_j = q(\hat{U}_j + \hat{M}_j)^\beta$	
T4.23	$\hat{u}_j = \hat{U}_j q_j$	$\hat{m}_j = \hat{M}_j q_j$
T4.24	$\hat{U}_{j+1} = \hat{U}_j - u_j$	$\hat{M}_{j+1} = \hat{M}_j - m_j$

Table 5
Median (80th percentiles) of proportional error in abundance estimates when fish are not marked.

Simulation model	Estimation model				
	Base	Schnute 2	Schnute 3	Escape	Density-dependent capture probability
Base	0.02 (−0.26, 0.87)	0.05 (−0.30, 1.94)	0.05 (−0.30, 1.94)	0.03 (−0.26, 0.86)	0.39 (−0.57, 1.43)
Hierarchy	−0.48 (-0.67, 0.53)	−0.43 (-0.70, 2.07)	−0.43 (−0.70, 2.07)	−0.18 (−0.63, 51.12)	−0.29 (−0.80, 0.60)
Exchange	−0.49 (−0.78, 151.32)	0.00 (−0.69, 199.62)	0.00 (−0.69, 243.75)	11.66 (−0.75, 154.83)	−0.18 (−0.69, 83.61)
Escape	−0.20 (−0.43, 0.08)	−0.19 (−0.45, 1.04)	−0.19 (-0.45, 104)	−0.05 (−0.34, 51.17)	−0.13 (−0.68, 0.92)
Individual	−0.10 (−0.28, 0.12)	−0.10 (−0.29, 0.30)	−0.10 (−0.29, 0.30)	−0.10 (−0.28, 0.15)	0.00 (−0.61, 0.77)

The final estimation model (Density dependent) assumed all fish were equally vulnerable to capture but capture probability varied with the total abundance of fish in the system at a rate set by the exponent β (T4.22; Peterman and Steer 1981, Hilborn and Walters 1992). Capture probability can decline (hyperdepleted; β > 1) or increase (hyperstable; β < 1) as fish are removed from the population. This model has three estamable parameters: N_o, q and β (T4.20). Abundance of marked and unmarked fish was calculated as the difference between estimated total abundance and the known number of marks (T4.21). Abundance of marked and unmarked fish declined due to removals (T4.23–T4.24).

The observations u_i and m_i from the removal processes were assumed to represent independent samples from Poisson distributions conditional on q, with means given by $\hat{u}_i$ and $\hat{m}_i$ respectively. This is equivalent to assuming independent binomial sampling of individuals in each of the unmarked and marked groups with sample capture probability q. The log-likelihood function (ignoring constants independent of model parameters) is

$$ln\mathcal{L}(u, m|\Theta) = \sum_{j}^{T} \left[-\hat{u}_j + u_j ln(\hat{u}_j) \right] + \sum_{j}^{T} \left[\hat{m}_j + m_j ln(\hat{m}_j) \right] \tag{3}$$

where Θ is the parameter vector to be estimated (Table 4).

In addition to the five removal estimation models, we evaluated the relative performance of a single-sample Petersen mark-recapture model, using only the first sampling event (Schwarz and Seber, 1999). The model was fit to the data using a binomial log-likelihood (ignoring constants independent of model parameters)

$$ln\mathcal{L}(u, m|\Theta) = ln\binom{\hat{u}_1 + \hat{m}_1}{\hat{m}_1} + \hat{m}_1 \ ln\left(\frac{n_{mark}}{N_0}\right) + \hat{u}_1 \ ln\left(1 - \frac{n_{mark}}{N_0}\right) \tag{4}$$

where Θ is the parameter vector to be estimated (Table 4).

2.4. Evaluation of models and scenarios

Each removal model was applied to data from each behavioral model to estimate abundance despite the simulated behaviors that affect aggregate capture probability. Three scenarios were used to evaluate the effect marking has on estimated abundance. The first scenario assumed that the population being evaluated was depleted over five sampling events and the catch in each event was used to estimate abundance. No fish were marked in this scenario. The second scenario assumed that 10% of the population was marked prior to the onset of the removal experiment (i.e. $M_0/N_0 = 0.1$). We assumed that marking had no effect on the behavior or capture probability of fish and that all other assumptions of mark-recapture held (Ricker, 1975; Seber, 1982). Additionally, we compared model performance between the removal estimators when fish are marked with a simple Petersen mark-recapture with only one sampling event (i.e. the base model with $T=1$) to evaluate whether performing a full removal experiment is necessary when fish are marked. The final scenario assumed 10% of the population was marked prior to the onset of the removal experiment (i.e. $M_0/N_0 = 0.1$), but fish were affected by the marking process in a similar way to their behavior in the removal process, as outlined in Section 2.2.

Again, we included a comparison with a simple Petersen mark-recapture model.

Each of the five behavioral individual-based simulation models was used to simulate catch data over the five sampling events. We assumed that the population is closed throughout sampling. Data were simulated using parameters randomly drawn from lognormal sampling distributions described in Table 3. Each estimation model was then used to estimate the abundance from each generated dataset. Performance of each estimation model was reported as the proportional error between simulated abundance from each behavioral model and estimated abundance. Model performance was evaluated using accuracy (median proportional error) and precision (range of proportional error).

3. Results

The first scenario investigated examined how abundance estimators perform when fish are not marked and fish exhibit behaviors that affect their availability to the gear. Removal estimation models produced relatively accurate (i.e., median proportional error generally fell within the −0.5 and 0.5 range; Table 5), but imprecise initial abundance estimates when fish were unmarked (Fig. 2). When the Base behavioral model was used, all depletion assumptions held and all estimation models produced unbiased estimates of abundance. Moreover, the precision and accuracy of abundance estimates improve as population abundance increases, even if capture probability is proportionately lower (Table S1). In all other behavioral models, mean capture probability declined between sampling events because vulnerable fish declined faster than the total population (Hierarchy, Exchange and Escape) or because more catchable fish were preferentially removed (Individual), generally causing underestimation of abundance. The Base estimation model was the most precise model, but consistently biased downwards if any behaviors affect assumptions. The Schnute 2 and Schnute 3 models were equivalent or slightly less accurate than the Base model, but performed badly if vulnerable exchange behavior (simulation model 3) was exhibited, with more than a quarter of estimated abundances overestimating by over 400%. The Escape estimation model yielded the lowest levels of precision, especially when fitted to data from the Hierarchy, Exchange, and Escape behavioral models. The density-dependent estimation model was the most accurate abundance estimate, but was less precise than the Base model. All models yielded precise abundance estimates when fitted to data from the Individual behavioral model, but the Density-dependent model was the only estimation model able to accurately estimate abundance in under this behavior (Fig. 2).

The second scenario assumed fish were marked prior to the removal experiment and all mark-recapture assumptions were met (e.g., all fish were equally likely to be marked; Table 6; Fig. 3). Across all behavioral models, removal of marked fish was an index of removals from the entire population, regardless of behaviors exhibited. The result is nearly unbiased population estimates. The Schnute 2, Schnute 3, and Density-dependent models each produced accurate and precise estimates of abundance, regardless of the behaviors affecting fish in the removal process. The Peterson mark-recapture model also produced very accurate mean abundance estimates, but with lower precision (Fig. 3;
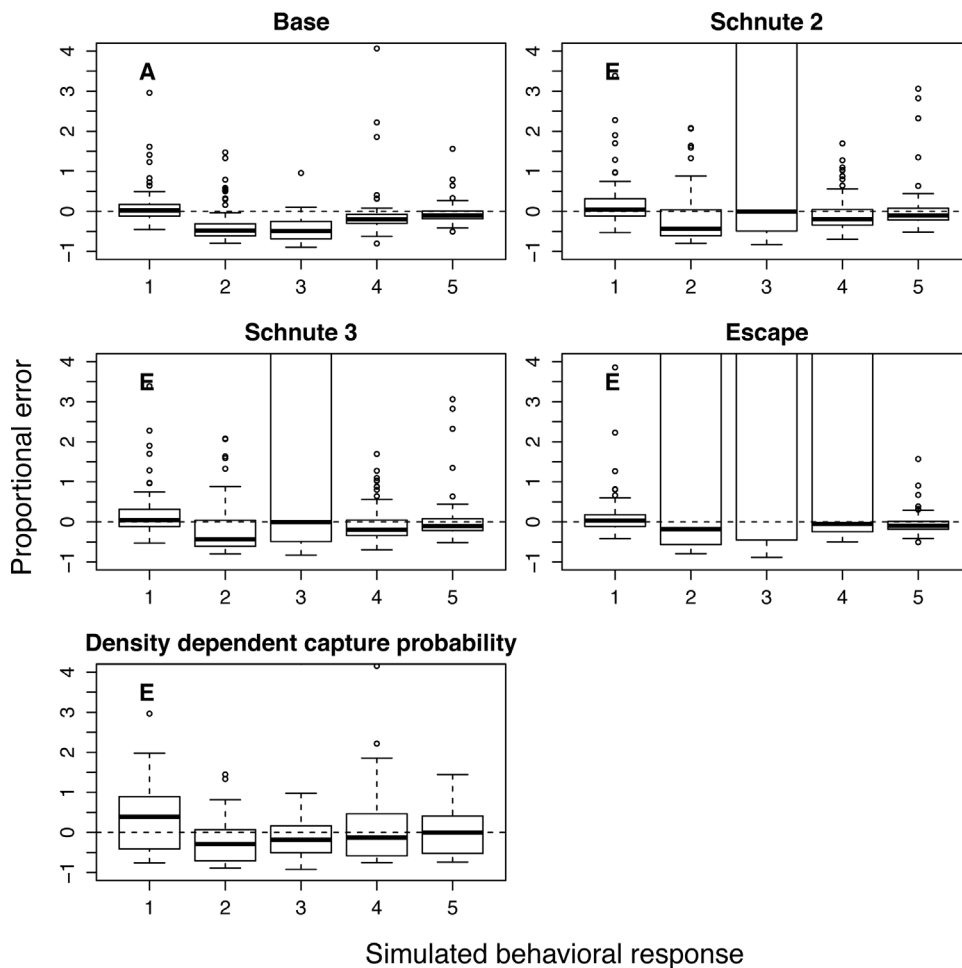
Fig. 2. Proportional error in initial abundance estimates obtained from five removal models. Removal models were fitted to data generated from five behavioral simulation models (x axis): 1 – Leslie model (Base model), 2 – Hierarchy model, 3 – Exchange model, 4 – Escape model, and 5 – Individual model, wherein capture probability varied among individuals. No fish were marked in this scenario. The population was depleted over five sampling events and catch in each event was used to estimate abundance.

bottom right).

The third scenario assumed fish were marked prior to the removal experiment, but fish behaviors affected the marking process in the same way as the removal process (i.e. vulnerable fish were vulnerable both to marking and removal). Performance of all estimation models in this scenario was variable and was highly dependent on the behavior exhibited (Table 7; Fig. 4). Marked fish became invulnerable prior to sampling in all behavioral models except Base and Individual, meaning the proportion of marked fish in the catch was much higher than in the population, resulting in overestimation of abundance. In the Individual behavioral model, fish with higher capture probability were marked and recaptured with the same probability, meaning abundance estimates were largely unbiased. When there was no change in behavior, and capture probability was constant or variable across individuals (i.e., Base and Individual behavioral models), all estimation models were more accurate (i.e., median error between −0.01 and 0.05) and precise (i.e., 80% range between −0.23 and 0.49) than when fish were

not marked (compare Figs. 2 and 4). However, all estimation models substantially and consistently overestimated abundance when fish react to the marking process (i.e. Hierarchy, Exchange and Escape models). Moreover, accuracy and precision was worse than if fish are not marked when fish exhibit these behaviors (see Fig. 2). The Base and Density-dependent capture probability models performed best overall, but still showed substantial overestimates, especially under the hierarchy simulated behavior. The Peterson mark-recapture estimation of abundance was more accurate than any other model when fitted to data from the Individual behavioral model, but performed worse overall when fish react to the marking process (i.e. Hierarchy, Exchange and Escape models; Fig. 4).

4. Discussion

The two objectives described were to show: 1) how a variety of fish behaviors will impact abundance estimates in removal experiments;

Table 6
Median (80th percentiles) of proportional error in abundance estimates when fish are marked and all fish have an equal probability of being marked.

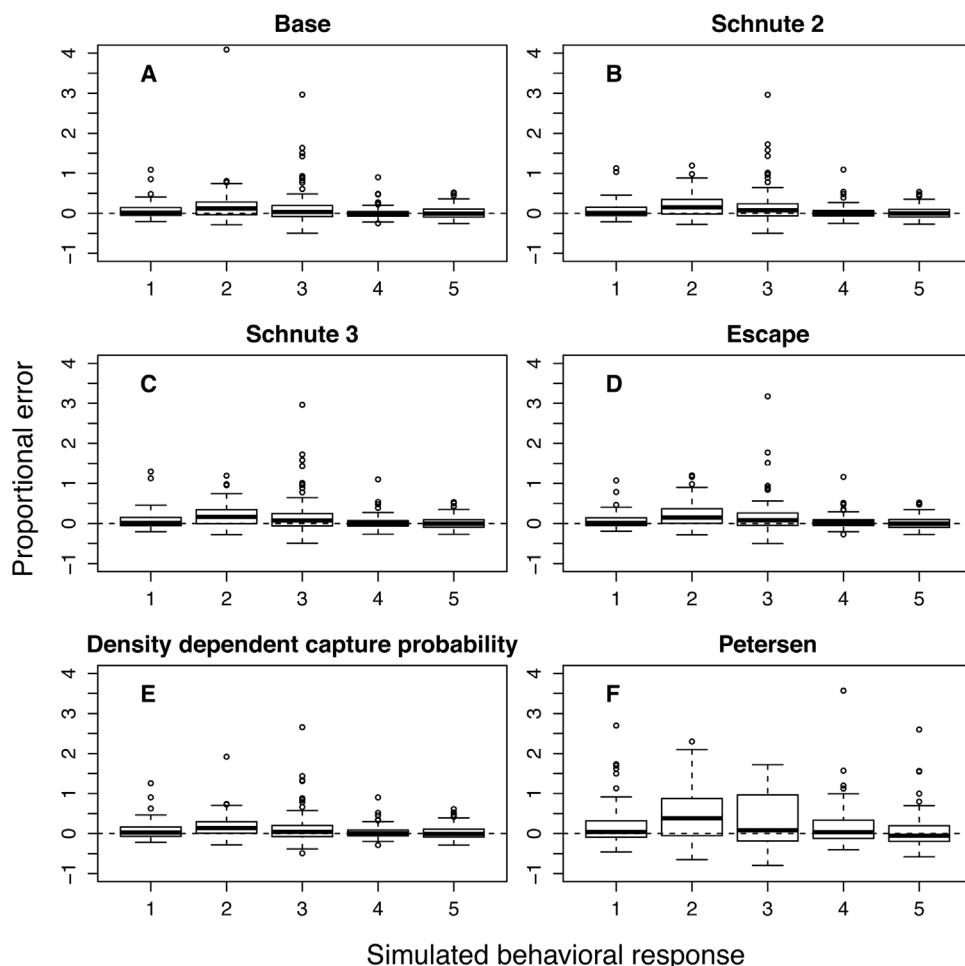| Simulation model	Estimation model					
	Base	Schnute 2	Schnute 3	Escape	Density-dependent capture probability	Petersen
Base	−0.02 (−0.18, 0.23)	0.00 (−0.19, 0.23)	0.00 (−0.19, 0.22)	−0.01 (−0.18, 0.20)	0.01 (−0.17, 0.23)	0.05 (−0.30, 1.01)
Hierarchy	−0.04 (−0.28, 0.41)	−0.01 (−0.26, 0.44)	−0.01 (−0.26, 0.44)	0.01 (−0.24, 0.37)	0.00 (−0.24, 0.37)	0.09 (−0.40, 2.23)
Exchange	−0.04 (−0.29, 0.25)	−0.01 (−0.27, 0.37)	−0.01 (−0.27, 0.37)	0.02 (−0.24, 0.37)	−0.05 (−0.27, 0.20)	0.10 (−0.39, 320.76)
Escape	0.00 (−0.18, 0.17)	0.03 (−0.15, 0.21)	0.03 (−0.15, 0.21)	0.06 (−0.15, 0.23)	0.05 (−0.16, 0.21)	−0.02 (−0.29, 0.83)
Individual	−0.06 (−0.17, 0.14)	−0.04 (−0.17, 0.19)	−0.04 (−0.17, 0.19)	−0.06 (−0.17, 0.14)	−0.02 (−0.17, 0.21)	0.00 (−0.27, 0.65)

Fig. 3. Proportional error in initial abundance estimates obtained from five removal models and a Petersen mark-recapture model. Removal models were fitted to data generated from five behavioral simulation models (x axis): 1 – Leslie model (Base model), 2 – Hierarchy model, 3 – Exchange model, 4 – Escape model, and 5 – Individual model, wherein capture probability varied among individuals. Ten percent (10%) of the population was marked prior to the onset of the removal experiment and the population was depleted over five sampling events. We assumed that all the assumptions of mark-recapture were met (Ricker, 1975). Catch in each event was used to estimate abundance.

and 2) evaluate whether abundance estimates can be improved when marked fish are used in removal experiments. Our study helps demonstrate that a variety of plausible fish behaviors affect capture probability across all estimation models examined, which has implications for abundance estimates. Of greater concern is the fact that animals are even more likely to display a combination of these transitory and persistent behaviors in a single study leading to highly variable probability of capture. Moreover, while using marked fish in the removal process substantially improved model performance if mark-recapture assumptions were met, estimated abundance may be more biased and/or imprecise than when fish were not marked (compare Figs. 2 and 4). Unfortunately, detecting violations in mark-recapture assumptions is difficult in most situations, making accuracy of abundance estimates uncertain.

A primary motivation to use removal methods is that they are relatively simple and only require a few data points (Meyer and High 2011). Our proposal to mark fish prior to conducting a removal study

calls into question the overall utility of doing the removal study at all in favour of simply implementing a single-sample mark-recapture study. We have shown the relative bias in abundance estimated using the Petersen model was intermediate between removal methods with and without marked fish when mark-recapture assumptions were met (Fig. 3). Under conditions where mark-recapture assumptions are violated, there was a notable reduction in the performance of the Petersen model, unless the only source of variation in capture probability is among individuals, rather than among sampling events (Fig. 4). This raises concerns about the utility of the single-sample mark-recapture study and indicates the need for a multiphase mark-recapture design if mark-recapture method were to replace the removal method. However, multiphase mark-recapture designs are usually labour intensive (Meyer and High, 2011). Therefore, from a sampling efficiency perspective, the removal method appears to be a viable option when a relatively robust model is used (such as the Density-dependent capture probability model). However, there may still be substantial underestimation of

Table 7
Median (80th percentiles) of proportional error in abundance estimates when fish are marked but only vulnerable fish are marked in proportion to their capture probability.

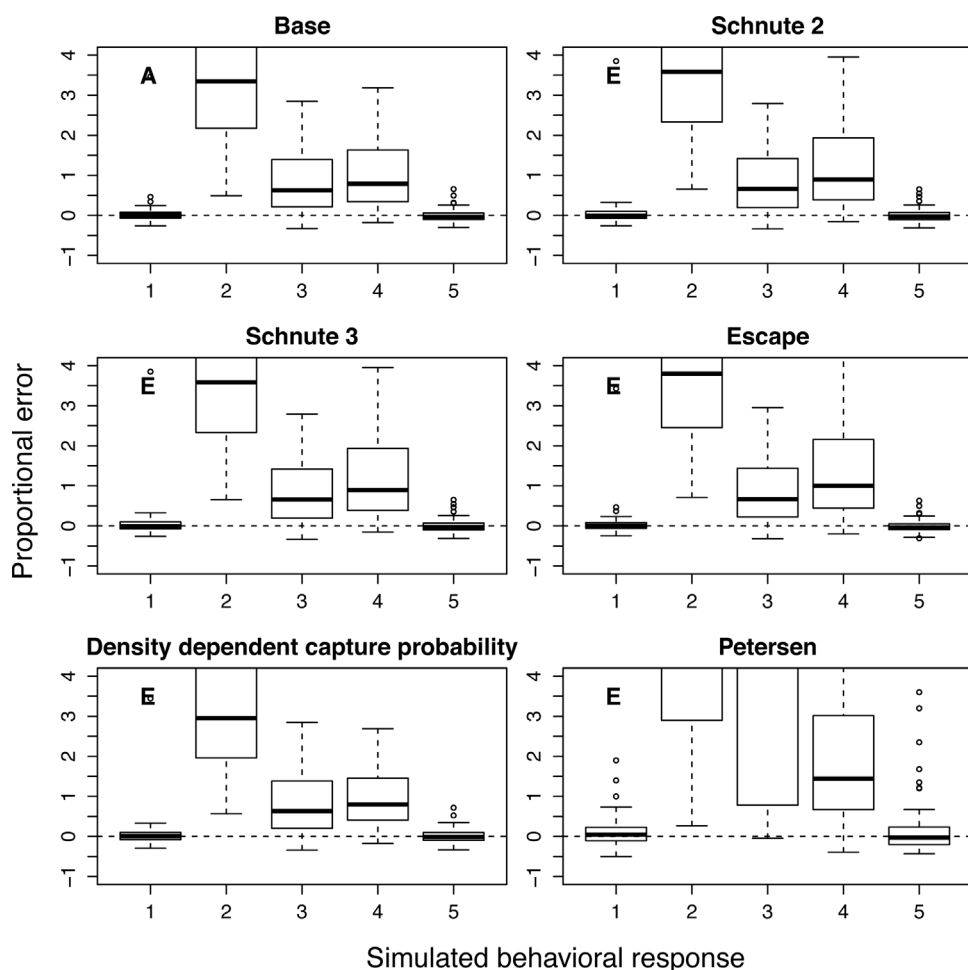| Simulation model	Estimation model					
	Base	Schnute 2	Schnute 3	Escape	Density-dependent capture probability	Petersen
Base	0.01 (−0.13, 0.16)	−0.01 (−0.11, 0.20)	−0.01 (−0.11, 0.20)	0.01 (−0.13, 0.16)	0.01 (−0.13, 0.19)	0.05 (−0.23, 0.49)
Hierarchy	3.34 (1.25, 298.13)	3.58 (1.41, 298.15)	3.58 (1.41, 298.15)	3.80 (1.45, 298.15)	2.95 (0.07, 2.33)	12.45 (1.08, 443.28)
Exchange	0.63 (0.07, 2.43)	0.66 (0.06, 2.47)	0.66 (0.06, 2.47)	0.67 (0.09, 2.49)	0.63 (0.07, 2.33)	45.23 (0.10, 585.85)
Escape	0.79 (0.14, 2.51)	0.89 (0.15, 2.86)	0.89 (0.15, 2.86)	1.01 (0.18, 3.14)	0.80 (0.19, 2.25)	1.44 (0.15, 7.21)
Individual	−0.03 (−0.15, 0.12)	−0.03 (−0.16, 0.15)	−0.03 (−0.16, 0.15)	−0.04 (−0.15, 0.11)	−0.01 (-0.17, 0.20)	−0.03 (−0.30, 0.52)

Fig. 4. Proportional error in initial abundance estimates obtained from five removal models and a Petersen mark-recapture model. Removal models were fitted to data generated from five behavioral simulation models (x axis): 1 – Leslie model (Base model), 2 – Hierarchy model, 3 – Exchange model, 4 – Escape model, and 5 – Individual model, wherein capture probability varied among individuals. Ten percent (10%) of the population was marked prior to the onset of the removal experiment and the population was depleted over five sampling events. Only vulnerable fish were marked, which removed them from the vulnerable population; thereafter the population recovered for 10 days prior to removal. Catch in each event was used to estimate abundance.

abundance depending on how fish behave in response to capture and handling.

For a removal model to truly estimate abundance in the face of behaviors that affect capture probability, it must be sufficiently flexible to mimic the aggregate effect of the behaviors. Schnute models 2 and 3 (Schnute, 1983) were able to estimate the escape process because these models somewhat mimic this behaviors (surprisingly better than the Escape estimation model). Likewise, the Density-dependent capture probability model was able to accurately and precisely estimate abundance when capture probability is constant over time but varies across individuals because it mimics this behavior (Hilborn and Walters, 1992). There are no estimation models that can recover the vulnerability exchange rates in the Hierarchy or Exchange behavioral models. It may be possible to recover these parameters with marked fish and the appropriate estimation model (one mimicking the behavior), but the accuracy of that method would have to be established experimentally (i.e., with known population sizes). Since the exact behavioral response (s) to fishing gear is often unknown the evaluation we have conducted, which explores performance across behaviors, is appropriate for identifying a model robust to violations in assumptions of equal capture probability. Overall, it appears that the Density-dependent capture probability is most robust to uncertainty in behavior, but may still be highly inaccurate depending on the behavior exhibited by fish. Unfortunately, the Density-dependent model comes at the cost of an additional parameter, which will likewise increase the minimum number of data points (removal periods).

Removal experiments can be adjusted to control for non-constant capture probability that is induced by removal apparatus or that is innate to an individual in the population (Carrier et al., 2009; Peterson et al., 2004; Rosenberger and Dunham, 2005). Our simulation mimicked an experimental design where a subset of the population was marked prior to the removal experiment. Including marked fish in removal models can potentially address the issue of non-constant capture probability and bias-correct abundance estimates (Yip and Fong, 1993), as long as fish do not react to the marking or removal process directly. Therefore, steps must be taken to minimise the effect of experimental apparatus on fish behavior. A key consideration in this experimental design is the choice between a single-gear and a dual-gear approach (Carrier et al., 2009). On one hand, the argument that a dual-gear approach will reduce bias (e.g., bias caused from trap response in subsequent sampling events) can be refuted by the argument that different gears have their own inherent biases. For example, gears might disproportionately capture animals in a specific age class (Finstad et al., 2000) or have different capture efficiencies (Rosenberger and Dunham, 2005). A dual-gear approach that utilizes sampling apparatus that maximise catch and reduce stress in the first pass while using a different gear that simply maximises catch in the subsequent catch events is one potential approach (Carrier et al., 2009). Recommendations pertaining to the choice of gear are outside the scope of this project but are an important consideration.

While several studies have used marking to evaluate variation in capture probability and use this to correct estimates of abundance (e.g., Rosenberger and Dunham 2005, Foley et al., 2015), incorporating marked fish directly into the estimation of abundance is relatively uncommon (although is gaining traction in commercial stock assessments; e.g., Cadigan, 2016), especially in small, closed populations. This 'one-step bias correction' is an efficient method for fixing abundance estimates, but is only effective if the only source of variation in capture

probability is between individuals. If fish react to being captured and marked such that they become invulnerable, marking fish result in a substantial overestimation of abundance. The severity of bias is directly proportional to the exchange rates between vulnerable and invulnerable states (v_1 and v_2; Online Supplemental Material). If these rates are high, there is very little bias and marking improves abundance estimates over what is possible with no marking. However, bias can be substantial with relatively low exchange rates so that fish do not quickly recover and become vulnerable. Establishing what the exact mechanism is that causes biased abundance estimates is rarely the purpose of removal experiments. Our results caution against concurrent marking and removal because the presence and nature of capture probability changes are largely unknown. Only if mark-recapture assumptions are shown to be met should marking be considered in a removal experiment (compare).

While we demonstrated that incorporating marked fish into removal methods could reduce bias in certain circumstances, we did not evaluate the likely situation where multiple behaviors interact. In addition to being a limitation of our study, the exclusion of multiple behavioral models also show that the extent of biases are likely more pronounced than what is shown here. Another limitation of our study manifests in the fact that we assumed a constant sample size despite the additional effort that would be expended to capture and mark fish prior to the removal experiment. In a real-word experiment with a fixed budget, resources would have to be diverted from the removal exercise. This would likely result in a smaller sample size and possibly wider confidence intervals.

Our study confirmed that stochastic behavior of fish in a population can pose challenges to the standard (Leslie) removal model, the suite of hybrid removal models and the Petersen mark-recapture model. This is a disconcerting situation since removal models are extensively used to estimate abundance for many valuable species. Integrating marked fish with the removal method did not prove to be a solution for the problem, neither for the complete suite of removal models nor for a single removal model. While we acknowledge our findings on using marked fish are specific to the behaviors we have evaluated, we feel it suggests a closer look at how marking data may impact abundance estimate should be investigated more closely in future applications. The Density-dependent capture probability model performed moderately better than other removal models evaluated here, but should only be used when fish are not marked unless there is confidence that mark-recapture assumptions are met. Surprisingly, our findings show that marking fish may just as easily confuse as improve abundance estimates and should be avoided without carefully considering assumptions.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.fishres.2017.06.010.

References

Benejam, L., Alcaraz, C., Benito, J., Caiola, N., Casals, F., Maceda-Veiga, A., De Sostoa, A., Garcia-Berthou, E., 2012. Fish catchability and composition of four electrofishing crews in Medeterranean streams. Fish. Res. 123–124, 9–15.

Bohlin, T., Sundström, B., 1977. Influence of unequal catchability on population estimates using the Lincoln index and the removal method applied to electro-fishing. Oikos 28, 123–129.

Cadigan, N.G., 2016. A state-space stock assessment model for northern cod, including under-reported catches and variable natural mortality rates. Can. J. Fish. Aquat. Sci. 73, 296–308.

Carle, F.L., Strub, M.R., 1978. A new method for estimating population size from removal data. Biometrics 34, 621–630.

Carrier, P., Rosenfeld, J.S., Johnson, R.M., 2009. Dual-gear approach for calibrating electric fishing capture efficiency and abundance estimates. Fish. Manag. Ecol. 16, 139–146. http://dx.doi.org/10.1111/j.1365-2400.2009.00657.x.

Cox, S.P., Beard, T.D., Walters, C., 2002. Harvest control in open-access sport fisheries: hot rod or asleep at the reel? Bull. Mar. Sci. 70, 749–761.

De Gisi, J.S., 1994. Year Class Strength and Catchability of Mountain Lake Brook Trout. MSc Thesis. University of British Columbia.

Finstad, A.G., Jansen, P.A., Langeland, A., 2000. Gillnet selectivity and size and age structure of an alpine Arctic char (Salvelinus alpinus) population. Can. J. Fish. Aquat. Sci. 57, 1718–1727.

Foley, K., Rosenberger, A., Mueter, F., 2015. Effectiveness of single-pass backpack electrofishing to estimate juvenile coho salmon abundance in Alaskan headwater streams. Fish. Sci. 81, 601–610. http://dx.doi.org/10.1007/s12562-015-0888-1.

Hilborn, R., Walters, C.J., 1992. Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty. Chapman and Hall, New York.

Kelso, J.R.M., Shuter, B.J., 1989. Validity of the removal method for fish population estimation in a small lake. North Am. J. Fish. Manag. 9, 471–476. http://dx.doi.org/10.1577/1548-8675(1989)009<0471:VOTRMF>2.3.CO;2.

Leslie, P.H., Davis, D.H.S., 1939. An attempt to determine the absolute number of rats on a given area. J. Anim. Ecol. 8, 94–113.

Mahon, R., 1980. Accuracy of catch-effort methods for estimating fish density and biomass in streams. Environ. Biol. 5, 343–360.

Mantyniemi, S., Romakkaniemi, A., Arjas, E., 2005. Bayesian removal estimation of a population size under unequal catchability. Can. J. Fish. Aquat. Sci. 62, 291–300. http://dx.doi.org/10.1139/F04-195.

Meyer, K.A., High, B., 2011. Accuracy of removal electrofishing estimates of trout abundance in Rocky Mountain streams. North Am. J. Fish. Manag. 31, 923–933. http://dx.doi.org/10.1080/02755947.2011.633684.

Peterman, R.M., Steer, G.J., 1981. Relation between sport-fishing catchability coefficients and salmon abundance. Trans. Am. Fish. Soc. 110, 585–593.

Peterson, N.P., Cederholm, C.J., 1984. A comparison of the removal and mark-recapture methods of population estimation for juvenile coho salmon in a small stream. North Am. J. Fish. Manag. 4, 99–102.

Peterson, J.T., Thurow, R.F., Guzevich, J.W., 2004. An evaluation of multipass electrofishing for estimating the abundance of stream-dwelling salmonids. Trans. Am. Fish. Soc. 133, 462–475.

Pollock, K.H., Hines, J.E., Nichols, J.D., 1984. The use of auxiliary variables in capture-recapture and removal experiments. Biometrics 40, 329–340.

Ricker, W.E., 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Canada 1913890, 382pp.

Riley, S.C., Fausch, K.D., 1992. Underestimation of trout population size by maximum likelihood removal estimates in streams. North Am. J. Fish. Manag. 12, 768–776. http://dx.doi.org/10.1577/1548-8675(1992)012<0768.

Rosenberger, A.E., Dunham, J.B., 2005. Validation of abundance estimates from mark-recapture and removal techniques for rainbow trout captured by electrofishing in small streams. North Am. J. Fish. Manag. 25, 1395–1410. http://dx.doi.org/10.1577/M04-081.1.

Schnute, J., Fournier, D., 1980. A new approach to length-frequency analysis: growth structure. Can. J. Fish. Aquat. Sci. 37, 1337–1351.

Schnute, J., 1983. A new approach to estimating populations by the removal method. Can. J. Fish. Aquat. Sci. 40, 2153–2169.

Schwarz, C.J., Seber, G.A.F., 1999. Estimating animal abundance: review III. Stat. Sci. 14, 427–456.

Seber, G.A.F., 1982. The Estimation of Animal Abundance and Related Parameters, 2nd ed. Edward Arnold, London.

Smith, M.T., Addison, J.T., 2003. Methods for stock assessment of crustation fisheries. Fish. Res. 65, 231–256.

Walters, C.J., Juanes, F., 1993. Recruitment limitation as a consequence of natural selection for use of restricted feeding habitats and predation risk taking by juvenile fishes. Can. J. Fish. Aquat. Sci. 50, 2058–2070.

Wyatt, R.J., 2002. Estimating riverine fish population size from single- and multiple-pass removal sampling using a hierarchical model. Can. J. Fish. Aquat. Sci. 59, 695–706.

Yamakawa, T., Yoshihara, M., Nishimura, M., Ohnishi, S., 1994. Expanded DeLury's method with variable catchability and its application to catch-effort data from spiny lobster gillnet fishery. Fish. Sci. 60, 59–63.

Yip, P., Fong, D.Y.T., 1993. Estimating population size from a removal experiment. Stat. Probab. Lett. 16, 129–135.