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# Assessment of biases in the estimation of tag shedding rates through a mark-resight experiment

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## ABSTRACT

Several flexible methods for estimating tag loss rates through mark-resight data have been developed recently. They allow evaluation of different tag shedding modalities and relax the usual assumption of independence between the loss of tags made in classical double-tagging methods. Two conditions limit the applicability of these methods: (1) tagged individuals must have permanent marks so that they can still be identified after losing their tags, and (2) a large number of observations is required to obtain precise estimates. Here we evaluate the performance of alternative estimators of tag shedding rates when these conditions are not met, a situation that is very common in mark-resight experiments on reef fishes. We simulated resighting data using a simple exponential model of tag shedding under different scenarios created by varying the probabilities of fish detection and fish emigration from the reef, and the tagging schedule. The model was conditioned on actual data from a short-term (~1.5 years) double-tagging study conducted on the Argentine sandperch *Pseudoperca semifasciata* (Cuvier 1829) in rocky reefs of northern Patagonia. We tested eight estimation procedures: three variants of an individual-based method, two based on a binomial likelihood function for exact or pooled times-at-liberty data, and three regression methods. Although the individual-based approach produced unbiased and most precise estimates when individuals that had lost both tags were identifiable, it performed poorly in the absence of permanent tags. In contrast, conditional methods, which do not require identification of individuals that have lost both tags, were more robust, providing unbiased and precise estimates. The pros and cons of the different methods for analyzing small-scale mark-resight experiments are discussed.

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## 1. Introduction

The individual identification of animals and the application of mark-recapture techniques are classic approaches for studying demography, life history and behavior of animal populations. Mark-resight methods, a variant of mark-recapture in which tags are “recaptured” via non-invasive sighting surveys (e.g. visual censuses, camera traps, radio tracking, etc.), are particularly useful for studying vulnerable species or species that inhabit protected areas or no-take reserves, as animals do not need to be killed to recover the tags. Those methods do not involve capturing and handling animals once they have been tagged; therefore, mark-resight techniques are generally less stressful for the animals and less expensive than traditional mark-recapture techniques because fewer and less trained personnel are needed, more data can be gathered in less time, and resights can be made while pursuing other research objectives (Minta and Mangel, 1989). This is particularly relevant in

studies of unexploited populations, in which the costs of recapturing the animals are provided almost exclusively by limited research funds (Castro and Rosa, 2005). A major limitation of mark-resight methods, however, is that they require identification of individuals or tag identities (e.g., through field-readable tags).

In the case of reef fishes, resightings are typically done by scuba diving, which further constrains the size, and spatial and temporal scales of the experiments: censused areas are usually much smaller than 1 km<sup>2</sup> and survey programs commonly last less than a year (e.g., Annese and Kingsford, 2005; Castro and Rosa, 2005; Corless et al., 1997; Zeller and Russ, 2000). Yet, these localized experiments can be informative about reef site fidelity, home range and small-scale movement of fishes, and their spill-over from marine reserves (e.g., Annese and Kingsford, 2005; Chapman and Kramer, 2000; Cole et al., 2000). The probability of detecting tagged individuals during surveys is reduced by temporary displacement of fishes engaged in foraging or reproductive activities out of the censused area, even if for brief periods, cryptic behavior of certain species, and poor visibility. In the absence of permanent marks, reductions in the number of total resightings resulting from tag shedding cannot be distinguished at first sight from those due to emigration, death or just failed detection. Accounting for tag loss is therefore essential

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to obtain unbiased estimates of population parameters, similar to any kind of mark-recapture experiment (Arnason and Mills, 1981).

The estimation of tag shedding rates poses particular problems in the case of localized, small-size mark-resight studies. Classical methods based on double tagging experiments (Beverton and Holt, 1957; Chapman et al., 1965; Seber, 1973, 1982), which use regression of recaptures over time, may not be suitable because they tend to require many recaptures (Kirkwood and Walker, 1984). The advantage of these methods is that they only use ratios of numbers of individuals recaptured with one and two tags, and are therefore robust to emigration, mortality and failed detection, provided these processes have the same rates for all tagged fish (Wetherall, 1982). However, the precision of the estimates still depends on the number of recaptures; hence disappearance of tagged fish, from whatever cause, would result in higher variances. Recaptures are often pooled by time intervals to increase their numbers, but this in turn may lead to different estimates depending on the time interval used (Xiao, 1996). The maximum likelihood method by Kirkwood and Walker (1984) was developed specifically to handle data-limited situations for which the classical methods are unsuitable.

All these earlier methods are based on two simplifying assumptions: the tag shedding rate is constant and the loss of one tag does not affect the probability that the other tag will be lost (i.e., independent tag loss). The latter assumption has been found to be violated in empirical studies (Bradshaw et al., 2000; Diefenbach and Alt, 1998; McMahon and White, 2009; Rivalan et al., 2005). In recent years, new methods for estimating tag loss through mark-resight experiments have been developed that do not depend on those assumptions. These methods were designed for long-term studies of pinnipeds (McMahon and White, 2009; Pistorius et al., 2000) and sea turtles (Rivalan et al., 2005), involving large numbers of resightings. Because in these experiments animals are not removed from the population and hence can be encountered multiple times, the estimation makes use of individual resighting histories. As a general rule, they use more complex mathematical models for describing tag shedding, including the effect of covariables (e.g., gender, age, or physiological condition) and a large number of parameters (e.g., up to 51 parameters in the multimodel framework proposed by McMahon and White, 2009). The estimation of such highly parameterized models requires large data sets with many tag shedding observations (Adam and Kirkwood, 2001). In addition, some of these techniques (e.g., Rivalan et al., 2005) require the use of permanent tags in order to distinguish individuals that have lost both tags from those that were never tagged. In this case, the tag shedding rate can be estimated for each tag separately, relaxing the usual assumption of tag independence (McMahon and White, 2009; Rivalan et al., 2005). In the absence of permanent tags, however, disappearance of tagged animals from causes other than tag loss may bias the estimates (see for example Oosthuizen et al., 2010).

In this paper we evaluate the performance of several methods for estimating tag shedding rates from mark-resight experiments in data-limited situations. We conducted a simulation study to test three classes of estimators: the individual-based method by Rivalan et al. (2005), specifically designed for analyzing mark-resight data, the classical regression methods based on aggregate recapture data (Chapman et al., 1965; Seber, 1973, 1982), and the maximum likelihood method by Kirkwood and Walker (1984). In the simulated scenarios the estimators were challenged by (a) sparse data, (b) lack of permanent marks, (c) use of repeated resightings instead of recaptures, and (d) violation of assumptions underlying the estimation procedures. Our operating model used to simulate data was based on an actual case study corresponding to a short-term (~1.5 years) double-tagging experiment conducted on the Argentine sandperch *Pseudoperca semifasciata* (Cuvier, 1829) (Pisces, Pinguipedidae), a species that lives in close association to rocky reefs in

**Table 1**

Synthesis of the eight estimation methods evaluated in this study.

Individual-based method by Rivalan et al. (2005); estimated by maximizing expression (2)
RIV <sub>full</sub> : full likelihood; uses $Q_{hij}$ , where $h=2, 1$ and $j=2, 1, 0$ .
RIV <sub>nz</sub> : no zeros; uses $Q_{hij}$ , where $h=2, 1$ and $j=2, 1$ .
RIV <sub>first</sub> : first-tag; uses $Q_{hij}$ , where $h=2$ and $j=2, 1$ .
Kirkwood and Walker (1984) method; solved by maximizing expression (5)
K&W <sub>exact</sub> : exact times at liberty.
K&W <sub>pool</sub> : pooled times at liberty (with 10, 20, 30, 40, 50, 60 and 100 day-intervals).
Regression methods based on Chapman et al. (1965) and Seber (1973, 1982); fitted by generalized linear models with Gaussian error and logarithmic link function
SEB <sub>ew</sub> : $w_t = 1$ (equal weighting); pooled times-at-liberty with 10, 20, 30, 40, 50, 60 and 100 day-intervals.
SEB <sub>nw</sub> : $w_t = n_t$ ; pooled times-at-liberty with 10, 20, 30, 40, 50, 60 and 100 day-intervals.
SEB <sub>vw</sub> : $w_t = (\sigma^2_{k_t} + 0.01/n_t)^{-1}$ ; pooled times-at-liberty with 10, 20, 30, 40, 50, 60 and 100 day-intervals.

the northern Patagonian coast. We evaluated the effects of different emigration rates, detection probabilities, tagging schedules and length of time intervals (in those methods that use pooled times at liberty) on the performance of the different approaches.

## 2. Materials and methods

### 2.1. Methods for estimating tag loss

We compared the performance of eight estimation methods, clustered in three groups (Table 1): (1) individual-based methods developed by Rivalan et al. (2005), referred to as RIV; (2) variants of Kirkwood and Walker's (1984) method, referred to as K&W; and (3) variants of a regression method based on Chapman et al. (1965) and Seber (1973, 1982), referred to as SEB. While the first two groups use exact times at liberty, SEB often requires pooling recaptures by time-at-liberty intervals. K&W can also be applied to pooled data, or to a mixture of exact and pooled times-at-liberty data. Both K&W and SEB methods assume that the tags are shed independently and that the probability of tag retention is the same for all tags.

### 2.2. Tag-shedding model

Because our objective was to find a robust and precise estimator for data-limited situations, in the absence of permanent tags, we used the simple tag-loss model formulated by Chapman et al. (1965). If a fish is tagged at time  $t=0$  and no immediate tag loss (Type I loss, Beverton and Holt, 1957) occurs, the probability of tag retention at time  $t$ ,  $k_t$ , decreases exponentially from an initial value of 1:

$$k_t = \exp(-\lambda t) \quad (1)$$

where  $\lambda$  is the instantaneous tag-shedding rate, assumed constant.

### 2.3. Individual-based (RIV) method

The RIV method uses a versatile expression to describe a wide variety of tag loss models, including up to five parameters per tag. In our application we used the simple exponential model (Eq. (1)) and assumed the same tag-shedding rate for both tags. Between consecutive resightings, a tagged individual may retain or lose one or both tags, if two were present. The particular sequence of observations over a series of resightings of the  $i$ th individual will be one of 11 possible tag-loss histories (see Appendix A). Its likelihood  $L_i$  can be calculated in terms of a set of probabilities  $Q_{22}$ ,  $Q_{21}$ ,  $Q_{11}$ ,  $Q_{20}$  and  $Q_{10}$ , where  $Q_{hij}$  is the probability that an individual observed with  $h$  tags has  $j$  tags at the following resighting, conditional on

the time elapsed between resightings (i.e.,  $Q_{22}$  is the probability of retaining both tags in a given time period,  $Q_{21}$  the probability of retaining only one having lost one tag and retaining the other, and so on; see Appendix A for further details). These probabilities are a function of the model parameters, which can be estimated by maximizing the sum of the individual log-likelihoods:

$$\ln L = \sum_{i=1}^N \ln L_i \quad (2)$$

where  $N$  is the number of resighted individuals. It is assumed that animals have a permanent mark so that all successive changes from two to zero tags remaining attached can be tracked. The likelihood function corresponding to this situation is here referred to as “full likelihood” (RIV<sub>full</sub>). In addition, we considered two different approaches for dealing with situations in which individuals that have lost both tags cannot be identified. The likelihood function in this case cannot use  $Q_{20}$  and  $Q_{10}$  because the loss of the second tag cannot be registered. The first approach, called “no-zeros” (RIV<sub>nz</sub>), uses all the data up to the last resighting to calculate (at most) the probabilities  $Q_{22}$ ,  $Q_{21}$  and  $Q_{11}$ . Oosthuizen et al. (2010) applied this approach for estimating tag loss rates in elephant seals. The second approach, called “first-tag” (RIV<sub>first</sub>), estimates  $\lambda$  based on the data only up to the loss of the first tag; the remaining tag serves only to indicate that the animal had been tagged. In this case, individual likelihoods are calculated at most from  $Q_{22}$  and  $Q_{21}$ .

#### 2.4. K&W method

Assuming that no differences exist between the tags attached to one individual, in the absence of permanent marks only two outcomes (‘one’ or ‘two’ tags) are possible when the animal is resighted after a given time at liberty. Following Kirkwood and Walker (1984), the probabilities that a fish resighted at time  $t$  since tagging bears one ( $p_{st}$ ) or two tags ( $p_{dt}$ ) are, respectively:

$$p_{st} = 1 - \frac{k_t}{2 - k_t} \quad (3)$$

and

$$p_{dt} = \frac{k_t}{2 - k_t} \quad (4)$$

where  $k_t$  is given by Eq. (1). Assuming that  $N$  tagged fish were recaptured at times  $t_i$  ( $i = 1, 2, \dots, N$ ), and defining:  $N_i^{(2)} = 1$ ,  $N_i^{(1)} = 0$  if the  $i$ th fish had two tags, and  $N_i^{(2)} = 0$ ,  $N_i^{(1)} = 1$  if it had only one, the log-likelihood of the observations conditional on the recapture times is:

$$\ln L = \sum_{i=1}^N \left[ N_i^{(2)} \ln \left( \frac{\exp(-\lambda t_i)}{2 - \exp(-\lambda t_i)} \right) + N_i^{(1)} \ln \left( 1 - \frac{\exp(-\lambda t_i)}{2 - \exp(-\lambda t_i)} \right) \right] \quad (5)$$

(Kirkwood and Walker, 1984). Expression (5) was formulated for a mark-recapture experiment in which fish are caught only once after they have been tagged. We adapted the K&W method to a mark-resight experiment by assuming that successive resightings of the same individual were independent, and by counting the time-at-liberty  $t_i$  as the time since the previous resighting of the same individual still carrying two tags. This is equivalent to considering that each fish recaptured with two tags is immediately released (see Pistorius et al., 2000). Hence, each individual fish may contribute more than one term in the likelihood depending on its resighting history. This method can be easily extended to a pooled times-at-liberty variant by grouping the resightings by arbitrarily chosen time intervals (see implementation in Section 2.10). In this paper

we tested both the exact (K&W<sub>exact</sub>) and the pooled (K&W<sub>pool</sub>) options.

#### 2.5. SEB method

If resightings made within each time interval are pooled, the assumptions leading to expression (5) correspond to a binomial likelihood for each  $t$ th time interval:

$$L_t = \binom{n_t}{n_{st} n_{dt}} \left( \frac{k_t}{2 - k_t} \right)^{n_{dt}} \left( 1 - \frac{k_t}{2 - k_t} \right)^{n_{st}}$$

(Wetherall, 1982: p. 692), where  $n_{st}$  and  $n_{dt}$  are, respectively, the number of resighted fish that retained one and two tags by the midpoint of the  $t$ th time interval, and  $n_t = n_{st} + n_{dt}$ . The maximum likelihood estimate of the probability of tag retention  $k_t$  based on the pooled observations in the  $t$ th time period is:

$$\hat{k}_t = \frac{2n_{dt}}{n_{st} + 2n_{dt}}$$

(Chapman et al., 1965, also derived by Seber (1973) under somewhat different assumptions) and its asymptotic variance can be estimated as:

$$\hat{\sigma}_{\hat{k}_t}^2 = \frac{\hat{k}_t(1 - \hat{k}_t)(2 - \hat{k}_t)^2}{2n_t}$$

(Wetherall, 1982). Unlike the RIV and K&W methods, this approach is not appropriate for more complicated tag shedding functions. We estimated  $\lambda$  by fitting the generalized linear model  $g(k_t) = -\lambda \tau_t$  (McCullagh and Nelder, 1989) to a series of  $\hat{k}_t$  estimates obtained for increasing times at liberty, using a logarithmic link function  $g(\mu) = \ln(\mu)$  and a Gaussian error structure; here  $\tau_t$  denotes the time elapsed since tagging to the midpoint of the  $t$ th time interval. We used three different weighting functions: (1) equal weightings (SEB<sub>ew</sub>); (2)  $w_t = n_t$  following Bayliff and Mobrand (1972) (SEB<sub>nw</sub>); and (3)  $w_t = (\hat{\sigma}_{\hat{k}_t}^2 + 0.01/n_t)^{-1}$ , i.e., the reciprocal of the variance of the tag retention probability plus a small positive term (SEB<sub>vw</sub>). The addition of a positive term is similar to that suggested by Fournier and Sibert (1990) within a robust estimation framework. In our case, it allowed inclusion of time intervals for which either  $n_{st}$  or  $n_{dt}$  was zero, and therefore  $\hat{\sigma}_{\hat{k}_t}^2 = 0$ . Fabrizio et al. (1996) applied a similar regression approach for estimating tag shedding in lake trout.

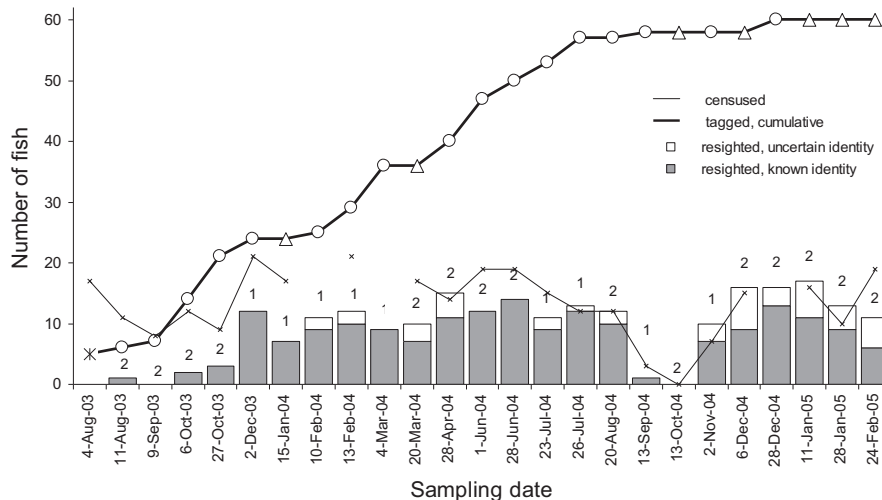
#### 2.6. Case study

The Argentine sandperch is a popular sport trophy fish in the northern Patagonian gulfs of Argentina, where it is found in coastal low-relief rocky reefs formed by small scattered fronts of hard substrate (Venerus et al., 2008). This species has been targeted by recreational anglers and spear-fishers for more than 60 years, and is also a tourist attraction for divers (Sanabra, 2002), mainly because of its large size (more than 1.20 m long and 25 kg weight). In 2001, a small-scale external tagging program was initiated in Nuevo and San José gulfs for studying its mobility and residence times on the reefs (Venerus, 2006). A double-tagging experiment was conducted as part of that tagging program.

#### 2.7. Mark-resight double-tag experiment

Sixty fish from a reef ledge off East Point, Golfo Nuevo, were double tagged between 4 August 2003 and 28 December 2004, over 18 fishing sessions (Fig. 1). Fish were caught with hand-lines (~19 h of soak time), measured to the lowest cm, tagged on board and immediately released. Exceptionally (5 fish on 4 August 2003), fish were pole-hooked and tagged underwater (Irigoyen





**Fig. 1.** *Pseudoperca semifasciata* tagged and resighted or hand-lined at the reef ledge off East Point. The symbols on the thick line (cumulative tagged fish) indicate the activities conducted in each sampling date: hand-line fishing only (asterisks), hand-line fishing and searching of tagged fish (open circles) and searching of tagged fish only (open triangles). The bars show resightings of tagged fish (doubtful fish identification in white). The numbers over the bars are the number of divers conducting the census in each sampling date. All sandperch (tagged and non tagged fish) were censused while swimming along the whole reef ledge.

and Venerus, 2008). One of us (L.A.V.) applied two external Floy<sup>TM</sup> FD-68B anchor tags to each fish using a code comprised of tag color, tag location along the dorsal fin (front, middle or back) and body side (left or right), to individualize tagged fish underwater. A second tag was added when fish were angled with only one tag, or two new tags were applied when the retained tag was difficult to read (and had to be cut to be read). Fish that had lost both tags were unidentifiable and, since Argentine sandperch may remain in the same reef for more than a year (Venerus, 2006), the probability of re-tagging the same fish was non-negligible.

Tagged fish were recovered through underwater resightings on 24 sampling occasions or by hand-line (Fig. 1), between 11 August 2003 and 24 February 2005. The period between successive visits to the reef ranged from 3 to 50 days (mean: ~24 days). In each underwater sampling, one or two divers roamed along the length of the reef (about 110 m) during 10–20 min, until no more tagged individuals were sighted. Additionally, all tagged fish sighted during focal sampling sessions conducted as part of a behavioral study were recorded. Divers registered the presence of tagged fish on plastic slates, along with their chromatic phenotypes (González, 2006), sizes in 10-cm TL classes, and tag location and color.

Counts of sandperch in East Point reef fluctuated seasonally, with minimum values in late winter and early spring (September–October), when fish disappeared from the reef coincidentally with the seasonal presence of dense thickets of the alien algae *Undaria pinnatifida* covering the reef ledges (Fig. 1, see also Irigoyen et al., 2011). Although very few tagged fish were resighted during these periods, particularly during the second year when the reduction in abundance was more pronounced (Fig. 1), 14 fish were tagged in October 2003.

All erroneous records ( $n=15$ ) in which the position and color of the tags did not match any of the possible combinations were excluded from the analysis. Besides, on 13 sampling dates, some fish resighted with one tag could not be identified unequivocally (Fig. 1). For each uncertain identity (19% of all resightings), we identified all possible candidates (based on fish size, and tag color and position) and constructed 500 possible tag-resighting matrices by bootstrapping among those candidate individuals. The tag shedding rate was estimated for each matrix using the eight methods explained above.

## 2.8. Simulated data

We constructed an operating model based on the simple exponential decay (Eq. (1)) to simulate a tag-resight experiment motivated by the Argentine sandperch study. The number of tagged fish ( $n=60$ ) and the sampling chronogram were similar to those used in reality, including 24 resighting events over 570 days. Tagged fish in the operating model may disappear from the reef by emigration and mortality, with combined constant risk  $r_{emi}$ . Fish that emigrate do not return. A tagged fish that is present in the reef at the time of a visual census can be detected with probability  $P_{det}$ , assumed to be homogeneous for all fish and independent of the number of tags attached. The determination of the number of tags attached is error-free; lack of detection merely increases the uncertainty about the timing of tag losses. The fate of each tag attached to each fish was treated independently for simulating the resighting histories.

The parameters  $r_{emi}$  and  $P_{det}$  were not estimated. Emigration and incomplete detection were included in the simulations so that fish could disappear from sight through processes other than tag loss, causing a form of censoring similar to the removal of study subjects in survival analyses (Klein and Moeschberger, 2003). In the absence of permanent marks, however, failing to resight an individual cannot be assigned to tag loss or emigration, and so the estimation cannot be adjusted for censoring. This problem affects the performance of RIV methods, which require that the entire process be observed up to the loss of the second tag.

We simulated a total of 20 scenarios by varying the tagging schedule, the values of  $r_{emi}$ ,  $P_{det}$  and the variance of  $\lambda$  among individuals (Table 2). Fish were tagged using two tagging schedules: all fish tagged at the beginning of the experiment (scenarios A1–A6) or fish tagged in sampling dates selected at random over the entire duration of the experiment, excluding the last sampling date (scenarios C9–C14) (Table 2).

We set the value of  $\lambda$  to  $0.0025 \text{ day}^{-1}$ , based on preliminary estimates obtained for the Argentine sandperch (Venerus, 2006). In order to evaluate the effects of heterogeneity among individuals, in scenarios B7 and B8 individual fish had different tag shedding rates which were sampled from a Gamma distribution (Kirkwood, 1981) with mean  $\bar{\lambda} = 0.0025 \text{ day}^{-1}$  and coefficient of variation equal to 0.25 (median and quartiles for the mean life time of a tag,  $1/\lambda$ , were 400, 258 and 706 days, respectively).

**Table 2**  
Specification of simulated scenarios.

Scenario #	Emigration rate (day <sup>-1</sup> ) ( $r_{emi}$ )	Detection probability ( $P_{det}$ )	Tag loss rate (day <sup>-1</sup> ) ( $\lambda$ )	Tagging schedule
A	1	1	0.0025	First day
	2	0.5		
	3	1		
	4	0.5		
	5	1		
B	6	0.5	$\lambda \sim \text{Gamma}; \hat{\lambda} = 0.0025;$ $CV = 0.25$	First day
	7	1		
	8	0.5		
	9	1		
	10	0.5		
C	11	1	0.0025	Random
	12	0.5		
	13	1		
	14	0.5		
	15	1		
D	16	0.5	0.0025	Ad hoc
	17	1		
	18	0.5		
	19	1		
	20	0.5		

We evaluated sensitivity of performance with respect to three values of  $r_{emi}$ , from zero to twice the value of  $\lambda$ , and two values of  $P_{det}$  (1 and 0.5) (Table 2). For the pooled time-at-liberty methods we tested seven different pooling intervals (see Section 2.10), which gives a total of 14,000 model runs for each scenario (i.e., 500 replicates  $\times$  4 methods  $\times$  7 intervals); thus, for computing time reasons, only the extreme combinations of  $r_{emi}$  and  $P_{det}$  for each tagging schedule were evaluated. Additionally, the combinations of  $P_{det} = 0.5$  and 1, and  $r_{emi} = 0$  and  $0.0050 \text{ days}^{-1}$  were simulated and analyzed using 10- and 100-day pooling intervals (see Section 3.1).

Finally, we included one ad hoc situation to represent the temporary absence of fish observed in late winter and early spring in our actual study case (scenarios D15–D20). In these scenarios, no recoveries were made during September–October, and fish were tagged in randomly selected surveys except during September–October of the second year, when no fish were tagged in reality (see Fig. 1).

We simulated 500 data sets for each scenario using routines programmed in R (R Development Core Team, 2008). The information content of the simulated data depends on the number of observations in each resight history. For example, in scenario A1 (Table 2), where the 60 tagged fish were released initially, and they were all present ( $r_{emi} = 0 \text{ day}^{-1}$ ) and detected ( $P_{det} = 1$ ) in every sampling date, all cells in the matrix of resighting histories contain a record of a fish with two, one or zero tags (Fig. 2). In contrast, in scenario D20, where the tagging schedule was ad hoc,  $r_{emi} = 0.0050 \text{ day}^{-1}$  and  $P_{det} = 0.5$ , only 13.1% of the cells in the matrix (on average) were filled, and 27% of the individuals tagged were never resighted, making a null contribution to the estimation of  $\lambda$ .

For the case of RIV<sub>full</sub> we also evaluated the sensitivity of the estimates to the fraction of tagged fish that are identifiable after having lost both tags. To do that, we used data from scenario A1, and assumed that none, all or half of the fish (selected at random) in each of the 500 data sets had permanent marks.

Overall, the simulated data sets departed in various ways from the ideal conditions for which each estimator was derived. Specifically: (i) small number of resightings challenges the pooled times-at-liberty methods (SEB and K&W<sub>pool</sub>); (ii) heterogeneity in tag loss rates among individuals (scenarios B7 and B8) violates the assumption that life times of tags are independent and identically distributed; (iii) the assumption that observations for different time periods are independent (built in the SEB and K&W methods) is violated by the use of repeated resightings; (iv) fish emigration results in censored data as fish disappear from the study before

the outcome is observed; (v) although permanent marks are not needed when the population is closed ( $r_{emi} = 0$ ) and  $P_{det} = 1$  (scenarios A1, B7, C9 and D15), the multinomial likelihood of RIV<sub>full</sub> cannot be computed exactly for the remaining scenarios (A2–A6, B8, C10–C14 and D16–D20).

## 2.9. Implementation of the estimation methods and optimization procedures

Since in our study only a few fish (1–7) were tagged and released in a given sampling date, the total number of resightings with one or two tags for increasing periods at large (used for K&W<sub>pool</sub> and SEB methods) were calculated by aggregating the resightings from all releases as if they came from a single tagged cohort (both in the simulated and in the real data sets) after discretizing the time after release in intervals of varying length, from 10 to 100 days. If an individual was resighted more than once during a given interval, we used the number of tags present at the last resighting, and assigned that number to the midpoint of the  $t$ th time interval ( $\tau_t$ ). This may introduce a small negative bias in the number of tags recorded.

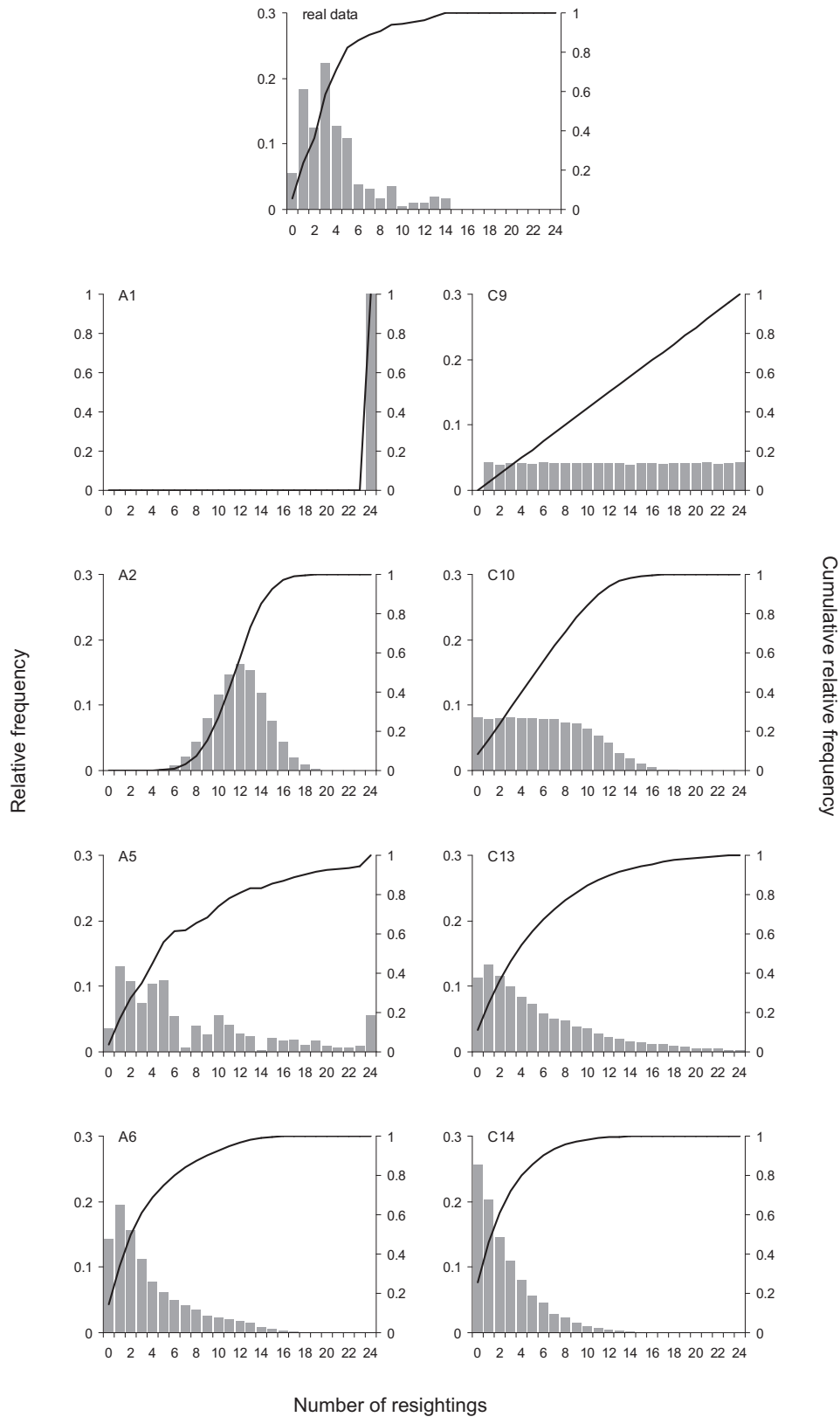
We coded the likelihood functions for the RIV and K&W methods using the R software (version 2.7.1, Development Core Team, 2008), and used the *optimize* routine from the *stats* package to maximize expressions (2) and (5). For both methods, the variance of  $\lambda$  was approximated by the negative inverse of the Hessian, evaluated at  $\lambda$ , and obtained by the *numDeriv* R package (Gilbert, 2006). Generalized lineal models for the SEB method were fitted with the *base* package of the R software.

## 2.10. Performance measures

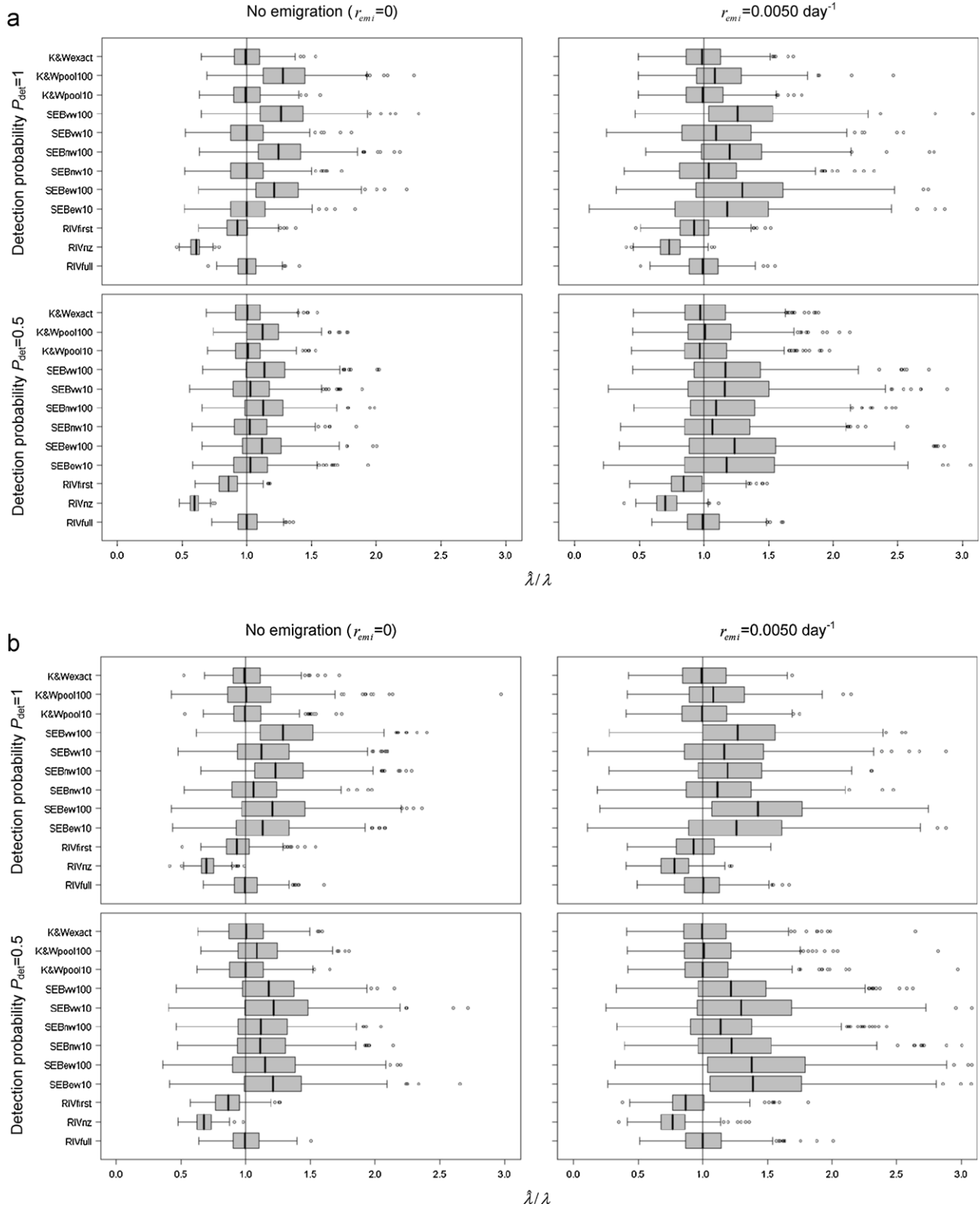
We evaluated the performance of the eight methods tested by means of the distribution of ratios between the estimates and the true value of the parameter from the operating model, represented graphically using Tukey's boxplots (Tukey, 1977). As a measure of bias we used the median relative bias (Magnusson and Hilborn, 2007):

$$\text{Median relative bias} = \text{median} \left( \frac{\hat{\lambda}_m - \lambda}{\lambda} \right)$$

where  $\lambda_m$  is the estimated value of the parameter for the data set  $m$ . The standard deviation among the estimates



**Fig. 2.** Relative frequencies and cumulative relative of the number of resightings per individual for the different scenarios simulated (indicated in the boxes) and for the real data set. The complete data matrixes for the simulated (60 fish  $\times$  500 data sets) and the real resight data (60 fish  $\times$  500 data sets in which doubtful recaptures were bootstrapped) were used to calculate the relative frequencies.



**Fig. 3.** Distribution of estimated tag shedding rates from simulated data, divided by the true value used to simulate the data. Panels show combinations of the two most extreme emigration rates tested and detection probabilities equal to 1 and 0.5. Each boxplot corresponds to the distribution of 500 estimates. The x-axis is truncated to avoid loss of detail. (A) Scenarios A1, A2, A5 and A6 and (B) scenarios C10, C11, C14 and C15.



for a particular simulation scenario was used to evaluate dispersion:

$$\delta = \sqrt{\frac{\sum_{m=1}^M (\hat{\lambda}_m - \bar{\hat{\lambda}})^2}{M}}$$

where  $\bar{\hat{\lambda}}$  represents the mean of the estimates and  $M$  the number of replicates. The standard error of the estimates (approximated by the negative inverse of the Hessian in RIV and K&W methods, and given by the glm routine of the R stats package in SEB methods) and the median of their coefficients of variation (CVs) were also evaluated.

### 3. Results

#### 3.1. Simulations

A total of 200,500 model runs were analyzed. The performance of the estimators varied markedly across scenarios, as indicated by the boxplots of the ratios of the estimates and the true value of  $\lambda$  (Fig. 3). Boxplots are shown only for scenarios A and C with the most extreme combinations of  $r_{emi}$  (0 and 0.0050 day<sup>-1</sup>) and  $P_{det}$  (1 and 0.5), and for 10 and 100-day time intervals in the case of SEB and K&W<sub>pool</sub>. Results for scenarios B and D (not shown) were qualitatively identical to those of scenarios A and C, respectively. In general, the performance of the estimation procedures degraded with a shortening of the period of resightings (due to emigration and/or random tagging schedules), and with a reduction in the detection probability. The exception was RIV<sub>nz</sub>, in which the median relative bias decreased with  $r_{emi}$  (Table 3A), and RIV<sub>full</sub> and K&W<sub>exact</sub>, in which median relative biases were negligible (i.e., less than 5%). Overall, RIV<sub>full</sub> and K&W<sub>exact</sub>, among the exact times-at-liberty methods, produced the most stable and least biased estimates in all scenarios (Fig. 3 and Table 3). K&W<sub>pool</sub> also produced unbiased results for most scenarios and time intervals, but led to positive bias under certain conditions (Fig. 4). Finally, the median relative biases of the pooled times-at-liberty methods varied in a rather unpredictable manner depending on the time intervals used for pooling the data (Fig. 4); their behavior was not uniform across scenarios.

The dispersion of the estimates increased with  $r_{emi}$  (Fig. 5) but was mostly unaffected by changes in  $P_{det}$  (Fig. 5; top vs. bottom row) or in the tagging schedules (compare Fig. 3A vs. B). The individual-based methods had lower dispersions in all scenarios, followed by the K&W methods; the SEB estimates had the highest dispersion (Table 3B). Conversely, K&W methods showed higher CVs, followed by RIV and SEB (Table 3C). Irrespective of the weighting function used, the standard error for the parameter estimate provided by the glm underestimated its variance (i.e., median of the standard error of the estimates was much smaller than the standard deviation among estimates, Fig. 5), resulting in lower CVs values with the SEB method.

Due to the differences in general performance of exact and pooled times-at-liberty methods, their results will be presented separately.

#### 3.2. Exact times-at-liberty methods (RIV<sub>full</sub>, RIV<sub>nz</sub>, RIV<sub>first</sub> and K&W<sub>exact</sub>)

The three individual-based methods tested differed in their performance (Table 3 and Fig. 3). The RIV<sub>full</sub> method was unbiased and performed best in all scenarios A–D, (median relative biases were less than 2%). However, its performance degraded as the fraction of fish with permanent marks (i.e., identifiable after having lost both tags) decreased (in the extreme, when individuals that have lost

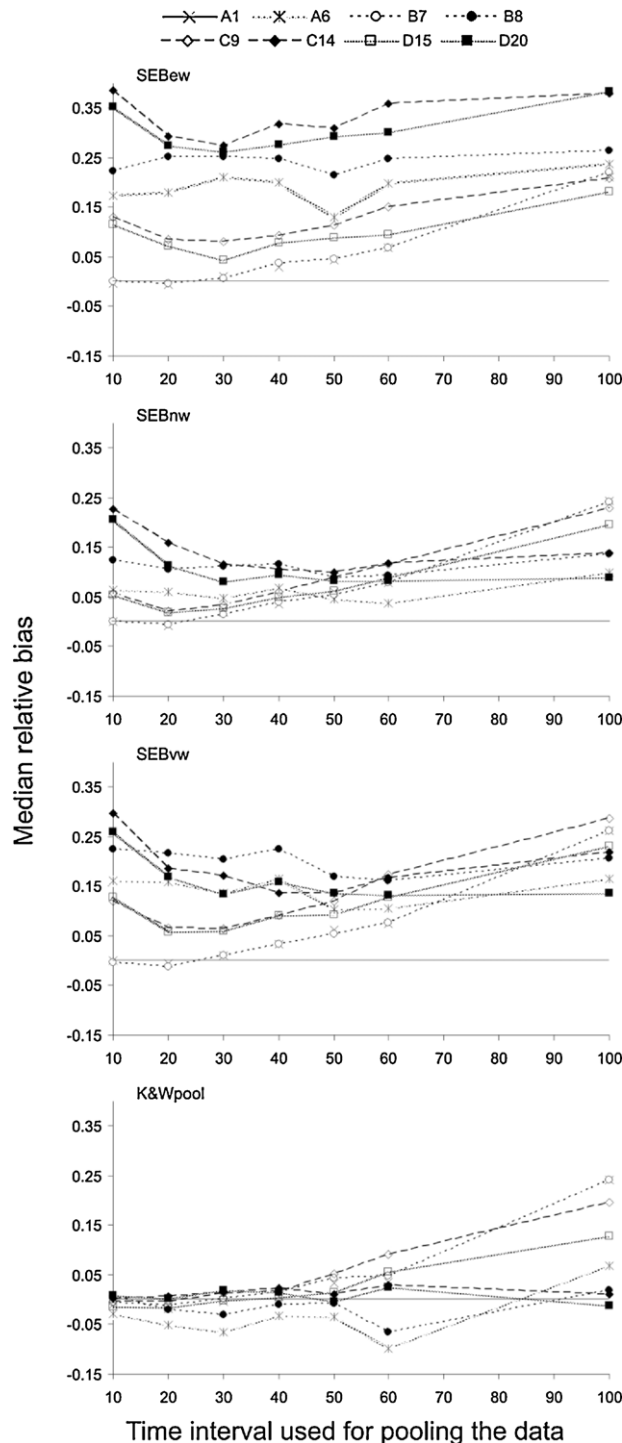


Fig. 4. Median relative bias obtained with the pooled times-at-liberty methods (SEB<sub>ew</sub>, SEB<sub>nw</sub>, SEB<sub>vw</sub> and K&W<sub>pool</sub>) using intervals from 10 to 100 days in different scenarios.

both tags cannot be identified, RIV<sub>full</sub> is equivalent to RIV<sub>nz</sub>) (Fig. 6). By contrast, RIV<sub>nz</sub> and RIV<sub>first</sub> systematically underestimated the tag shedding rate, the former producing the largest negative biases among all the methods tested (median relative bias in the range –0.22 to –0.41). As RIV<sub>first</sub> uses the resighting histories only up to the loss of the first tag to estimate  $\lambda$ , its estimates had lower bias (particularly for  $P_{det} = 1$ ) and were rather insensitive over the range of emigration rates examined, although they degraded with lower detection probabilities (Table 3). The RIV<sub>nz</sub> estimates had the lowest  $\delta$  among all the methods tested (Table 3 and Fig. 5).

**Table 3**

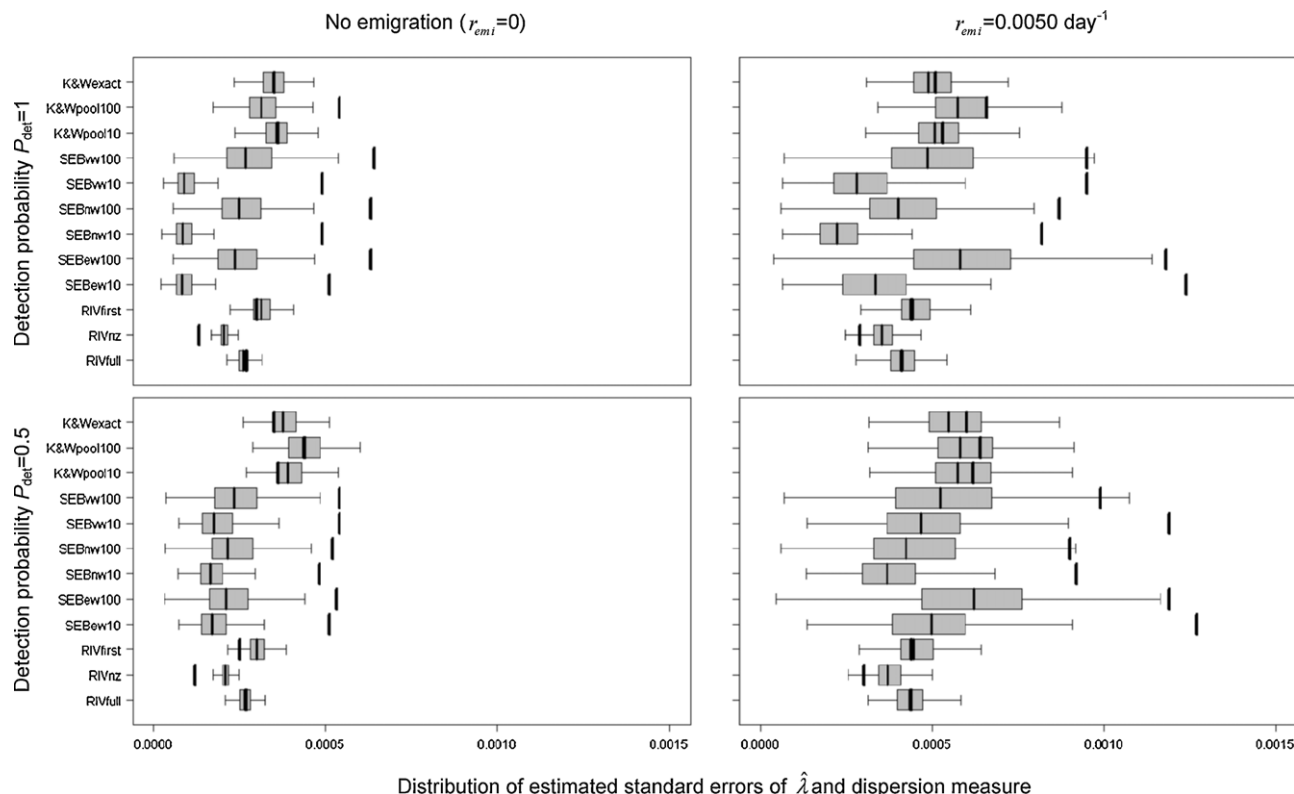
Results obtained with the eight methods tested in scenarios defined in Table 1. A: median relative bias; B: standard deviation among estimates ( $\delta$ ); and C: median coefficient of variation (CV). RIV<sub>full</sub> was applied assuming 100% of fish had permanent marks. Results for the pooled times-at-liberty methods correspond to 50-day time interval. The tag shedding rate used for simulating data was 0.0025 day<sup>-1</sup> in scenarios A, C and D, and had a Gamma distribution with mean 0.0025 day<sup>-1</sup> and CV = 0.25 in B (see Section 2.9 for details). Asterisks indicate absolute median relative biases between 0.05 and 0.10 (\*), and >0.10 (\*\*).

Scenario	$r_{emi}$ (day <sup>-1</sup> )	$P_{det}$	RIV <sub>full</sub>	RIV <sub>nz</sub>	RIV <sub>first</sub>	K&W <sub>exact</sub>	SEB <sub>ew</sub>	SEB <sub>nw</sub>	SEB <sub>vw</sub>	K&W <sub>pool</sub>
<b>A</b>										
A1	0	1	-0.004	-0.395**	-0.074*	-0.010	0.044	0.060*	0.063*	0.034
A2	0	0.5	0.000	-0.406**	-0.144**	0.001	–	–	–	–
A3	0.0025	1	-0.001	-0.319**	-0.065*	0.001	–	–	–	–
A4	0.0025	0.5	0.016	-0.321**	-0.122**	0.029	–	–	–	–
A5	0.0050	1	-0.005	-0.269**	-0.074*	-0.011	–	–	–	–
A6	0.0050	0.5	-0.009	-0.297**	-0.157**	-0.024	0.129**	0.047	0.103**	-0.034
B7	0	1	-0.001	-0.392**	-0.070*	-0.006	0.047	0.055*	0.055*	0.043
B8	0.0050	0.5	-0.002	-0.286**	0.132**	0.002	0.215**	0.090*	0.170**	-0.009
C9	0	1	-0.010	-0.306**	-0.072*	-0.004	0.114**	0.088*	0.120**	0.052*
C10	0	0.5	-0.006	-0.323**	-0.134**	0.001	–	–	–	–
C11	0.0025	1	-0.007	-0.249**	-0.066*	-0.005	–	–	–	–
C12	0.0025	0.5	-0.000	-0.280**	-0.126**	0.002	–	–	–	–
C13	0.0050	1	-0.005	-0.216**	-0.070*	-0.009	–	–	–	–
C14	0.0050	0.5	0.001	-0.232**	-0.128**	-0.005	0.310**	0.099*	0.137**	0.010
D15	0	1	-0.007	-0.320**	-0.109**	-0.019	0.090*	0.061*	0.092*	0.015
D16	0	0.5	-0.004	-0.328**	-0.163**	0.005	–	–	–	–
D17	0.0025	1	0.000	-0.269**	-0.091*	-0.004	–	–	–	–
D18	0.0025	0.5	0.008	-0.284**	-0.146**	0.013	–	–	–	–
D19	0.0050	1	0.001	-0.224**	-0.085*	-0.002	–	–	–	–
D20	0.0050	0.5	-0.007	-0.249**	-0.150**	0.002	0.292**	0.083*	0.136**	-0.004
<b>B</b>										
A1	0	1	0.00027	0.00013	0.00030	0.00035	0.00052	0.00050	0.00051	0.00039
A2	0	0.5	0.00027	0.00012	0.00025	0.00035	–	–	–	–
A3	0.0025	1	0.00034	0.00021	0.00039	0.00045	–	–	–	–
A4	0.0025	0.5	0.00036	0.00021	0.00034	0.00047	–	–	–	–
A5	0.0050	1	0.00041	0.00029	0.00044	0.00051	–	–	–	–
A6	0.0050	0.5	0.00044	0.00030	0.00044	0.00060	0.00120	0.00087	0.00104	0.00060
B7	0	1	0.00028	0.00014	0.00033	0.00039	0.00055	0.00054	0.00055	0.00043
B8	0.005	0.5	0.00045	0.00030	0.00043	0.00058	0.00115	0.00083	0.00096	0.00057
C9	0	1	0.00033	0.00020	0.00036	0.00042	0.00086	0.00064	0.00068	0.00047
C10	0	0.5	0.00035	0.00021	0.00034	0.00046	–	–	–	–
C11	0.0025	1	0.00038	0.00025	0.00039	0.00045	–	–	–	–
C12	0.0025	0.5	0.00044	0.00030	0.00044	0.00059	–	–	–	–
C13	0.0050	1	0.00049	0.00035	0.00050	0.00057	–	–	–	–
C14	0.0050	0.5	0.00053	0.00037	0.00049	0.00066	0.00148	0.00101	0.00120	0.00070
D15	0	1	0.00033	0.00019	0.00033	0.00041	0.00085	0.00060	0.00066	0.00045
D16	0	0.5	0.00034	0.00021	0.00031	0.00046	–	–	–	–
D17	0.0025	1	0.00042	0.00029	0.00044	0.00054	–	–	–	–
D18	0.0025	0.5	0.00043	0.00028	0.00038	0.00054	–	–	–	–
D19	0.0050	1	0.00049	0.00035	0.00048	0.00058	–	–	–	–
D20	0.0050	0.5	0.00051	0.00037	0.00047	0.00065	0.00140	0.00095	0.00115	0.00066
<b>C</b>										
A1	0	1	0.105	0.135	0.135	0.140	0.047	0.048	0.050	0.143
A2	0	0.5	0.106	0.140	0.140	0.151	–	–	–	–
A3	0.0025	1	0.136	0.164	0.164	0.171	–	–	–	–
A4	0.0025	0.5	0.140	0.174	0.174	0.187	–	–	–	–
A5	0.0050	1	0.164	0.192	0.193	0.200	–	–	–	–
A6	0.0050	0.5	0.177	0.209	0.209	0.223	0.173	0.137	0.162	0.224
B7	0	1	0.105	0.136	0.136	0.140	0.048	0.049	0.052	0.143
B8	0.005	0.5	0.175	0.209	0.209	0.225	0.170	0.136	0.160	0.226
C9	0	1	0.132	0.160	0.160	0.165	0.108	0.076	0.088	0.168
C10	0	0.5	0.140	0.172	0.172	0.184	–	–	–	–
C11	0.0025	1	0.160	0.186	0.186	0.192	–	–	–	–
C12	0.0025	0.5	0.174	0.204	0.204	0.218	–	–	–	–
C13	0.0050	1	0.186	0.209	0.209	0.217	–	–	–	–
C14	0.0050	0.5	0.204	0.236	0.236	0.253	0.217	0.174	0.209	0.256
D15	0	1	0.133	0.160	0.160	0.168	0.114	0.079	0.095	0.171
D16	0	0.5	0.138	0.169	0.169	0.184	–	–	–	–
D17	0.0025	1	0.160	0.189	0.189	0.197	–	–	–	–
D18	0.0025	0.5	0.170	0.204	0.204	0.221	–	–	–	–
D19	0.0050	1	0.189	0.218	0.218	0.227	–	–	–	–
D20	0.0050	0.5	0.209	0.243	0.243	0.260	0.237	0.189	0.226	0.262

The estimates obtained with K&W<sub>exact</sub> were unbiased in all scenarios (median relative biases ranged between -0.024 and 0.029), but slightly more variable than those obtained with the individual-based methods (Table 3 and Fig. 5). Median CVs were similar to those obtained with RIV<sub>nz</sub> and RIV<sub>first</sub> in all scenarios tested, although slightly larger (range: 0.14–0.26).

### 3.3. Pooled times-at-liberty methods (SEB<sub>ew</sub>, SEB<sub>nw</sub>, SEB<sub>vw</sub> and K&W<sub>pool</sub>)

The SEB methods tended to overestimate  $\lambda$  (Table 3A). When the results obtained with its three variants and all the time intervals tested were pooled, the median relative biases



**Fig. 5.** Distribution of the standard error of the estimates and standard deviation among estimates ( $\delta$ ) (thick bars) from simulated data for scenarios A1, A2, A5 and A6. Panels show combinations of the two most extreme emigration rates tested and detection probabilities equal to 1 and 0.5. Each boxplot and each bar corresponds to the distribution of 500 estimates. Outliers are not drawn to simplify the plot.

estimated for each scenario exceeded 0.15 in 38% of the cases and 0.20 in 26% (Fig. 4). In some cases it was not possible to fit an exponential model to the estimates  $\hat{k}_t$ , a problem that was more severe with low number of resightings and longer time

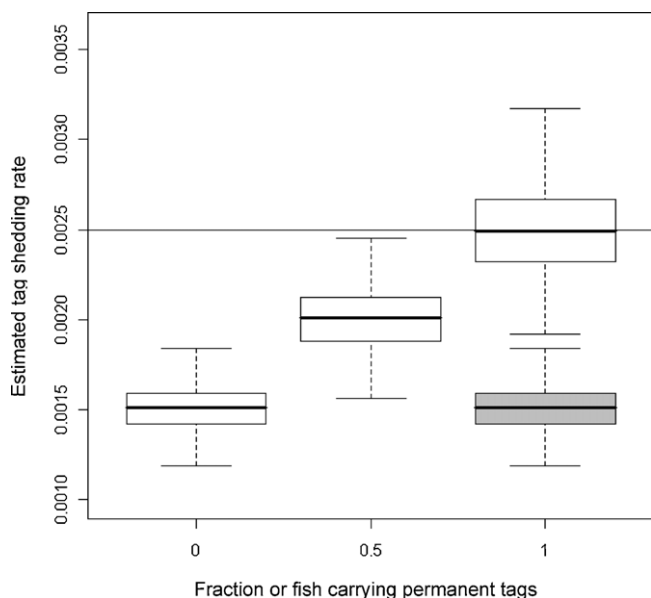
intervals (up to 15% of the replicates with SEB<sub>ew</sub> and 100-day intervals).

The positive median bias was largest when estimates were equally weighted in the regression (SEB<sub>ew</sub>) and they increased with random tagging dates, longer time intervals, higher emigration rates and smaller detection probabilities, with maximum median biases in the range 0.275–0.386 in scenario C14 (Fig. 4). Performance of SEB<sub>nw</sub> and SEB<sub>vw</sub> was better: more consistent results across scenarios were obtained with intermediate time intervals, from 30 to 60 days for SEB<sub>nw</sub>, and from 50 to 60 days for SEB<sub>vw</sub> (range of median relative biases: 0.014–0.117 for SEB<sub>nw</sub> and 0.055–0.174 for SEB<sub>vw</sub>). Some limited simulations conducted using a much larger number of tags ( $n = 1000$ , results not shown) indicated that positive biases were substantially reduced, being negligible for the shorter size classes, particularly in SEB<sub>nw</sub> and SEB<sub>vw</sub>.

All variants of the SEB methods were outperformed by K&W<sub>pool</sub>, which resulted in negligible bias (<5%) in most cases. K&W<sub>pool</sub> produced unbiased results with the smaller time intervals (10–50 days) in almost all scenarios. Only when the largest time interval (100 days) was used did some of the scenarios result in more than 20% overestimation (in median) (Fig. 4). The standard deviation of the estimates ( $\delta$ ) was smallest for K&W<sub>pool</sub>, followed by SEB<sub>nw</sub>, SEB<sub>vw</sub> and SEB<sub>ew</sub> (Fig. 5).

### 3.4. Sandperch application

A total of 184 individually identified resightings (including 31 hand-line recaptures) were made during 24 visual censuses and 18 fishing sessions conducted in East Point reef between 11 August 2003 and 24 February 2005 (range: 0–14 tagged fish resighted per sampling date) (Fig. 1). Another 44 resightings could not be unequivocally identified (from 1 to 7 fish resighted per sampling



**Fig. 6.** Boxplots for tag shedding rate estimates ( $\hat{\lambda}$ ) obtained with RIV<sub>full</sub> (white boxes) as a function of the fraction of fish that had permanent marks. Each box corresponds to 500 simulated data sets each containing 60 resighting histories. Estimates obtained with RIV<sub>nz</sub> (gray boxes), which are independent of the fraction of fish permanently marked, are included as reference. The line at 0.0025 day<sup>-1</sup> indicates the true value of tag-shedding rate used to simulate the data.

date), hence the identity of those fish was sampled from between 2 and 8 possible candidates per fish. A few fish could be identified after they had lost both tags, either from permanent scars or because additional tags had been applied, but the proportion was too small for  $RIV_{full}$ . The maximum number of certain resightings for a fish was 14, and the longest time at large was 507 days (Fig. 2). Some of the tagged sandperch that disappeared from the reef during late winter and early spring reappeared in mid spring and early summer (November–December), once *Undaria* fronds started to decompose (Irigoyen et al., 2011).

Based on our simulation results, the most reliable estimate of tag shedding should be that obtained with  $K\&W_{exact}$ :  $\lambda = 0.0040 \text{ day}^{-1}$  (CI 95%: [0.0038; 0.0042]).  $RIV_{first}$ , the only applicable individual-based method, resulted in  $\lambda = 0.0029 \text{ day}^{-1}$  (CI 95%: [0.0027; 0.0030]), and even lower estimates were obtained with  $RIV_{full}$  ( $\lambda = 0.0025 \text{ day}^{-1}$ ) and  $RIV_{nz}$  ( $\lambda = 0.0022 \text{ day}^{-1}$ ) (Table 4).

## 4. Discussion

### 4.1. Simulation-estimation results

The simulations showed that the individual-based estimates that use the complete tag-resighting histories ( $RIV_{full}$ ) are the preferred choice (unbiased and most precise) for situations in which fish that have lost both tags can be unequivocally identified. As the fraction of permanently tagged individuals decreases, the estimates become negatively biased. This is due to the inclusion in the likelihood of observations of repeated resightings of animals that retain a single tag, not balanced by those that lose it, which go unregistered. In these situations, our results indicate that it is preferable to use only the observations up to the first tag loss ( $RIV_{first}$ ) than to include all the resightings ( $RIV_{nz}$ ). The latter was the approach used by Oosthuizen et al. (2010), which has a large negative bias. To address this problem, Rivalan et al. (2005) applied PIT tags to a small fraction of tagged turtles (41 from a total of 2053 females tagged), and fitted the model in two steps: first, they selected the tag loss function for the second tag based on the loss of the first tag, and second, they estimated model parameters for the first and second tags independently, using only the subset of individuals with PIT tags to estimate the tag-shedding rate of the second tag. As a result, the uncertainty about the loss rate of the second tag was greater than that of the first (see confidence intervals in their Fig. 3).

A major disadvantage of  $RIV_{first}$  was that its performance degraded most rapidly when the number of re-sightings decreased due to emigration, low probability of detection, or irregular sampling schedule. By contrast,  $K\&W_{exact}$  was the only unbiased estimator in all scenarios. Even though  $K\&W_{exact}$  and  $RIV_{first}$  both use the individual resighting histories up to the loss of the first tag to estimate the tag shedding rate, the latter resulted in much larger negative biases. This can be explained in terms of the assumed likelihoods. While  $K\&W$  is based on a binomial outcome (one or two tags) conditioned on having resighted a tagged fish, the individual-based methods assume a multinomial distribution in which fish can be resighted bearing two, one or zero tags. In  $RIV_{first}$ , the terms of the log-likelihood involving events after the loss of the first tag are simply dropped, including successive resightings of a fish still bearing one tag. While this reduced the bias relative to  $RIV_{nz}$ , there is a fraction of animals – those that lost both tags between consecutive resightings – for which the loss of the first tag is not registered. Although few tag resighting histories fell in this category ( $Q_{20}$ ) in our simulations (<8.6%) they had an impact on the bias. Furthermore, given that in the absence of permanent tags only fish with one or two tags can be detected, the conditional binomial likelihood built into  $K\&W$  is the correct one.

The SEB methods mostly over-estimated  $\lambda$ . When time intervals were too short, and hence  $\hat{k}_t$  values were estimated from few resightings (say,  $n_t < 10$ ), the ratios were frequently zero (when no fish bearing two tags were resighted in a given time interval) or one (when all resighted fish carried two tags) (Fig. 7). Given that the mean life-time of a tag in our simulations was 400 days, more than one order of magnitude greater than the length of the smaller time intervals tested (10–20 days), the estimated tag retention probabilities  $\hat{k}_t$  were often equal to one for the initial periods after release, and tended to zero at increasing periods at large. This resulted in overestimation of  $\lambda$ , which worsened when all time periods were given equal weights in the regression ( $SEB_{ew}$ ). On the other hand, when intervals are long, underestimation of the number of tags may result from assigning the numbers registered during the last resighting to the midpoint of the time interval. In our simulations, this effect was most acute with larger number of resightings, causing larger positive biases in scenarios with no emigration and full detection when using weighted regression ( $SEB_{nw}$  and  $SEB_{vw}$ ) (Fig. 4).

### 4.2. Tag-shedding rate in Argentine sandperch

The estimates obtained using the different methods are ranked in an order that is consistent with the biases indicated by the simulation results, with the individual based methods resulting in the lowest estimates, followed by  $K\&W$  and then by SEB (Table 4).

The most reliable estimate of tag-shedding rate obtained with  $K\&W$  ( $\hat{\lambda} = 0.004 \text{ day}^{-1}$ ) corresponds to a mean tag life of 252 days (~8.4 months), about 60% of the value estimated with  $RIV_{full}$  (400 days). This tag life is short relative to the reef residence times observed for sandperch (uncorrected for tag loss), which often exceeded one year, reaching up to 867 days (Venerus, 2006). This emphasizes the importance of correcting for tag loss for estimating rates of emigration and potential spill-over from reefs.

Other studies in which rocky reef fishes were marked with external tags also reported rather high shedding rates. Culver (1987) estimated a tag shedding of up to 37.5% in black rockfish (*Sebastes melanops*) over ~7 months, a value lower than that estimated for *P. semifasciata* in this study (56.5% over 7 months). Rodgers and Wing (2008) evaluated tag loss in *P. colias* by maintaining 25 fish in outdoor tanks. Only 12% lost their tags over 225 days; however, it would be difficult to extrapolate those results to the wild. Finally, Irigoyen (2010) estimated lower tag loss shedding rates  $\hat{\lambda} = 0.0012 \pm 0.0002 \text{ day}^{-1}$  for the Argentine sea bass (*Acanthistius patachonicus*) using the same T-tags applied in this study.

Booth and Weyl (2008) discussed the causes of tag loss, including the physical characteristics of the environment, fishes' behavior and immunological response to the tag, tag design, suitability of the species for tagging, and tagging technique. *Pseudoperca semifasciata* lives strongly associated with rocky outcrops and spends much time inside crevices (Venerus and Irigoyen, unpublished data), with a preference for low-relief refuges with only one entrance (Galván, 2008). These characteristics could enhance the chances of tags being detached. Besides, the Argentine sandperch has a massive, rounded trunk which makes it difficult to anchor the T-bar tag correctly behind the pterygiophores, especially in larger individuals.

### 4.3. Performance of methods for estimating tag-shedding in small-scale experiments

Pooled times-at-liberty methods are widely used for estimating tag shedding rates, and they offer an obvious approach for increasing the number of recoveries per time interval in small-scale studies. The practice however has been criticized for several reasons. First, resulting estimates of tag-shedding rate may be

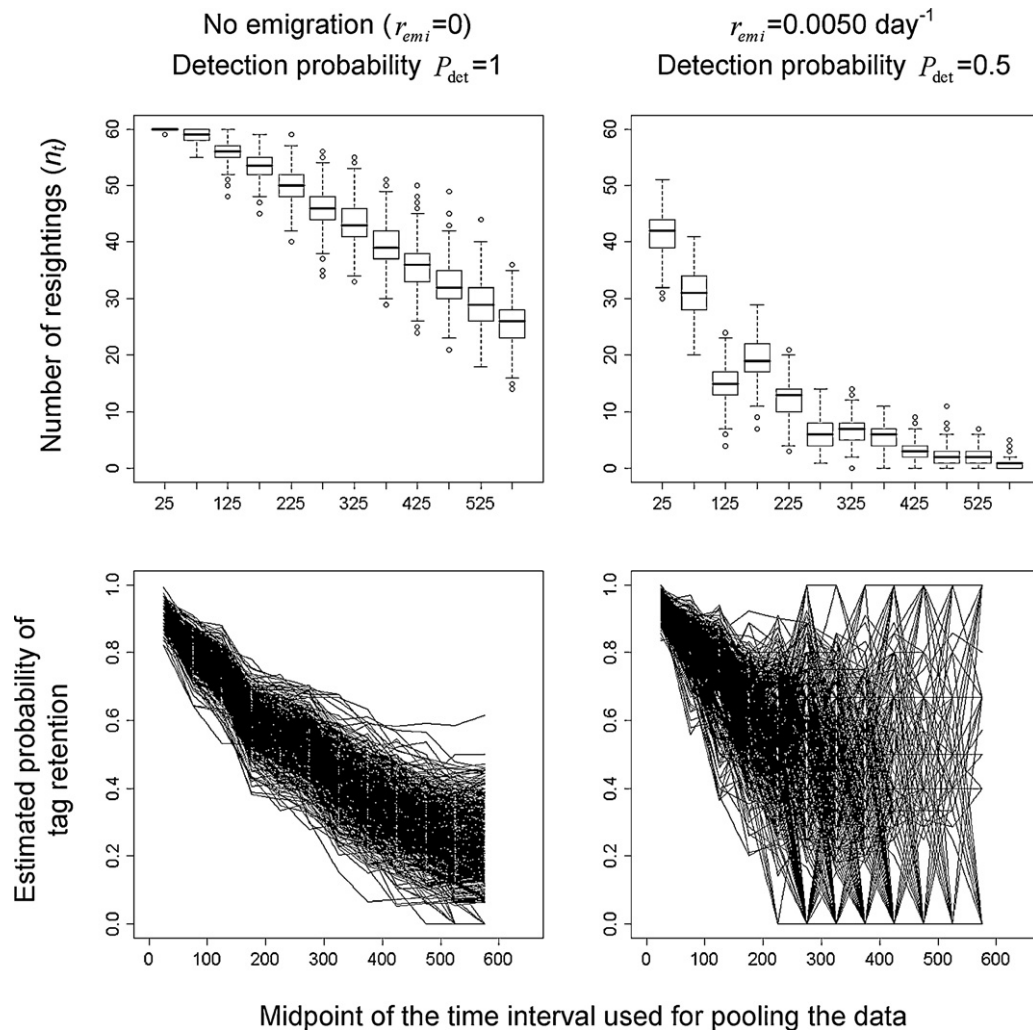
**Table 4**  
Instantaneous tag shedding rates estimated for the Argentine sandperch data with the eight methods. For the pooled time-at-liberty methods, the range of median estimates obtained with 10-, 20-, 30-, 40-, 50-, 60- and 100-day time intervals, are shown. Confidence intervals (95%) are indicated between brackets.

Method	Median tag shedding rate ( $\text{day}^{-1}$ )
Pooled time-at-liberty	K&W <sub>pool</sub>
	SEB <sub>ew</sub>
	SEB <sub>nw</sub>
	SEB <sub>vw</sub>
Exact time-at-liberty	K&W <sub>exact</sub>
	RIV <sub>full</sub>
	RIV <sub>first</sub>
	RIV <sub>nz</sub>

sensitive to the choice of time interval (Xiao, 1996). This situation arises when recoveries are few and irregularly spaced over time (Kirkwood and Walker, 1984), as was the case in our study. To address this problem, Fabrizio et al. (1996) used wider intervals for pooling the data at longer times at large so as to have at least 10 recoveries per interval (Wetherall, 1982). However, this procedure adds uncertainty about the actual number of tags attached at the midpoint of the longer time intervals. As discussed above, assigning the number of tags seen during the last resighting to the midpoint of the time interval may underestimate the number of tags and in turn overestimate  $\lambda$ . Other methods for assigning individual tag counts

to the midpoint of the interval may be tested in order to reduce these biases (e.g., by using the number of tags attached during the resighting that was closest to the midpoint of the interval). Overall, the number of resightings in each time interval should be considered before applying the SEB method, particularly in data-limited situations. Markedly improved performance may be achieved by weighting the  $\hat{k}_t$  estimates by the number of resightings. In any case, the lowest tag shedding rate estimate obtained with SEB over a range of time intervals may provide a rough upper-bound for  $\lambda$ .

Another disadvantage of the pooled times-at-liberty methods is that the rates of mortality, emigration and tag shedding are



**Fig. 7.** Number of resightings and estimated tag retention probabilities ( $\hat{k}_t$ ) ( $n=500$  for each plot) at increasing time since tagging (pooling interval = 50 days) in two different scenarios: no emigration and detection probability  $P_{det}=1$  (A1: left), and emigration rate  $r_{emi}=0.0050 \text{ day}^{-1}$  and  $P_{det}=0.5$  (A6: right). The small number of resightings at increasing periods at large makes estimates unstable in the latter.



all assumed to be constant over time (Xiao, 1996), which may be invalid. As noted by Kirkwood and Walker (1984), mortality rates must be constant within the time interval, but may differ between periods. However, in our study, because time at large was estimated for each individual fish by counting the days since tagging irrespective of the tagging date, we were forced to assume that mortality and emigration rates were both constant over the whole study period. Further simulations would be needed to evaluate how varying rates of emigration, mortality, etc., could affect the performance of pooled times-at-liberty methods.

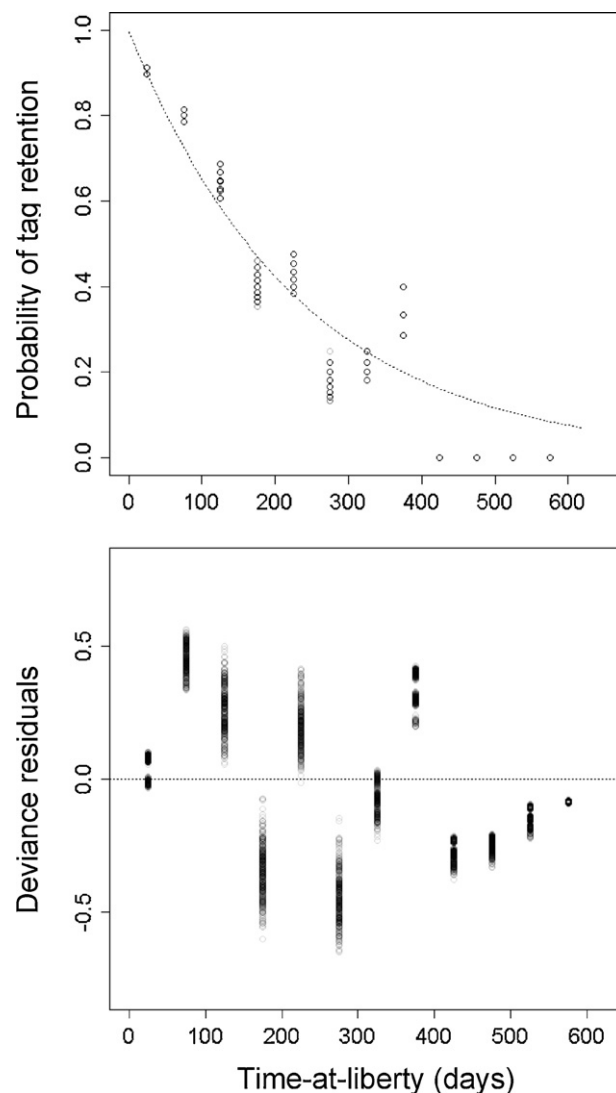
With reference to ratio methods, Pistorius et al. (2000) argued that bias may arise if multiple resights of an individual are used to estimate the probabilities of tag loss (as was done in this study). They also argued that care should be taken to include in a single  $\hat{k}_t$  estimate only those animals that had been at liberty during the same period since tagging (or since the last resighting with two tags in mark-resight experiments). Despite the fact that in our experiment tags were applied in different dates, individual identification of fish allowed us to pool the data by time at liberty intervals irrespective of the actual tagging date. However, this carried its own problems, as explained earlier.

Despite these caveats, an advantage of the pooled times-at-liberty methods is that they are more robust to fish identification problems. Because fish identification is only used to determine time-at-large intervals when different batches of tags are released at different dates, misidentification of animals released in the same batch, or within a period shorter than the pooling interval, do not affect the estimates. When all tags are released at once (or when batches can be distinguished, for example, by tag color) individual identification is not required.

In our experiment, the reliability of tag identification by scuba decreased with time since tagging because the external tags became fouled by algae and other encrusting organisms after a few months, mainly during spring and early summer. Uncertainty in the detection of tag color resulted in 15 fish that could not be correctly identified. Willis and Babcock (1998) noted that the ability of divers to correctly identify tag colors was affected by water clarity when using visible implant fluorescent elastomers, and that some misidentifications were common (error rate up to 20%); divers confused certain colors systematically, such as red and orange, or green and yellow. Quantification of the effects of confounding tagged individuals in the estimation of tag loss, however, has not received sufficient attention in the literature (but see Kendall, 2004).

In the absence of permanent individual marks, our results pointed to  $K\&W_{\text{exact}}$  as the best option for estimating  $\lambda$  in small-scale mark-resight experiments. If the exact times-at-liberty are unknown, resightings should be pooled using the smallest possible time interval to reduce the uncertainty about the timing of the first tag loss (Kirkwood and Walker, 1984). Given that  $K\&W_{\text{pool}}$  gave unbiased results for most scenarios, and that it allows incorporation of different tag loss functions (Kirkwood and Walker, 1984), it should be preferred over the SEB methods, provided individuals could be identified.

The operating model used in our simulations, based on a constant risk of tag shedding and independent tag losses, is admittedly oversimplified. However, constant-rate models may be adequate for short-term experiments (Kirkwood, 1981). Fabrizio et al. (1996) concluded that long-term and short-term tag-shedding rates may be described by different processes, and that Chapman's model could be used to adequately characterize tag shedding in the first 4–5 years after tagging. Robson and Regier (1966) could not reject the hypothesis of a constant tag shedding rate in a three-year mark-recapture experiment conducted on the lake whitefish *Coregonus clupeaformis*. For the case presented here, the evaluation of diagnostic plots based on glm results suggests that the simple exponential decay is a fairly reasonable model for describing the probability of



**Fig. 8.** Observed and fitted (dotted line) probabilities of tag retention (upper panel), estimated with the glm analysis (SEB<sub>new</sub> method, time interval = 50 days). Corresponding deviance residuals are shown below. Scattered dots represent 500 datasets in which doubtful recaptures were bootstrapped (see the text for details).

tag retention in *P. semifasciata*, at least during the first 1.5 years after tagging (Fig. 8). Indeed, the case studies we found in the literature in which models with time-dependent tag-shedding rates were favored, correspond to long-term mark-recapture experiments that spanned between 5 and 23 years (see for example Cadigan and Bratney, 2003, 2006; Kirkwood, 1981; Oosthuizen et al., 2010; Pistorius et al., 2000; Rivalan et al., 2005).

The possible dependence between the loss of tags is also a problem, but it cannot be evaluated without permanent marks. Recent studies provided evidence of a correlation between tags resulting from heterogeneous individual attributes (Bradshaw et al., 2000; Diefenbach and Alt, 1998; McMahon and White, 2009; Rivalan et al., 2005). In all of these studies the probability of losing the second tag once the first tag was lost was greater than would be expected under tag independence. Lack of independence results in greater-than-expected proportions of animals with two or zero tags, and in a deficit of animals retaining only one tag for extended periods (Oosthuizen et al., 2010). The dependence between tags in fish studies has been addressed by allowing the tag shedding rate to vary among individuals (Kirkwood, 1981). In addition, differences between taggers (Hearn et al., 1987) or between batches

of releases (Hearn et al., 1991) have also been detected. Although the same person tagged all fish in our study, reducing potential causes of heterogeneity, fish were tagged in different positions along the dorsal fin, and with tags of different colors. The latter could add heterogeneity if, for example, some tag colors differentially attracted other fishes that in turn could attack and remove the tags. Cadigan and Brattey (2003, 2006) found highly significant differences in the tag retention probability between two tags inserted on the same side of a fish, spaced only 3 cm apart. The low number of fishes tagged in our experiment, typical of the small-scale experiments considered in this study, precludes evaluation of the effects of tag location on retention probability. No information is available about other potential sources of heterogeneity between individuals related to their condition, immunological status, sex, age or behavior. On the other hand, when the tag shedding rate was assumed to be Gamma distributed in our simulations (scenarios B7 and B8), representing a moderate level of heterogeneity among individuals, the performance of the eight methods tested did not differ greatly from the scenarios in which  $\lambda$  was constant. Nevertheless, efforts should be made to include permanent marks in mark-recapture and/or in mark-resight experiments in order to improve estimates of tag shedding rates and in turn other vital rates, as recommended by Diefenbach and Alt (1998), McMahon and White (2009), and Oosthuizen et al. (2010).

A variety of methods have been used for marking fishes permanently: panjet tatoos, freeze branding, passive integrated transponders (PIT) and visible implant elastomers (VIE) (e.g., Dietrich and Cunjak, 2006; Josephson et al., 2008; Murray and Fuller, 2000; Rude et al., 2011; Zeller and Russ, 2000). Most of these marks are not strictly permanent, but they persist long enough to be useful to complement external plastic T-tags or dart tags in short-term double-tagging experiments. The long-term retention rates and visibility of implant elastomers have been little studied. Although retention rates are expected to vary between species, taggers and tag location,<sup>1</sup> high retention rates were reported for salmonids (Josephson et al., 2008). The main drawback of these techniques is their limited use for underwater mark-resight surveys, as mark detection usually requires a close and careful examination of the individuals. Although some alternatives have been developed in recent years to use PIT tags underwater (e.g., Jørgensen et al., 2005; Lauzon-Guay and Scheibling, 2008), the detection range varies with the position and orientation of the tag with respect to the antenna coil, and detection could be difficult in fast-swimming fishes (Meynecke et al., 2008).

The use of natural marks/scars for individual identification is also possible in many species (through, for example, photographic identification; see Castro and Rosa, 2005; Reisser et al., 2008; Speed et al., 2007). In the Argentine sandperch, females and juvenile yellow males present a clear pattern of brownish spots and lines in the head (González, 2006), which could potentially allow fish identification by means of pattern recognition software (e.g., Interactive Individual Identification System I<sup>3</sup>S<sup>2</sup>). Gray individuals (older males), however, characterized by the absence of spots after a short transition phase (González, 2006; Venerus, 2006), cannot be individualized in the same way.

In terms of the tagging schedule, efforts should be made to tag as many individuals as possible at the beginning of the double-tagging experiment in order to reduce the uncertainty around the estimates, and to justify the assumptions of equal rates of mortality and emigration for all fish tagged. If tagged individuals cannot be identified, which would preclude the use of individual-based and

K&W methods, increasing the number of tagged animals should reduce the bias of ratio-based estimators of  $\lambda$ .

Most of the estimation procedures tested were affected by changes in the emigration rates, detection probabilities and/or tagging schedules. The total number of resightings, and in turn the information content of the data, was reduced by both increasing  $r_{emi}$  and decreasing  $P_{det}$ . The reduction however was larger when  $r_{emi}$  was set to  $0.0050 \text{ day}^{-1}$  than when  $P_{det}$  was set at 0.5, and therefore the variance of the estimates was larger in the former case. Given that both the rate of emigration and the probability of detection are generally unknown, it could be difficult to predict a priori the magnitude of the biases and the variances of estimates from different methods. Notwithstanding, the simulation results presented are valuable for deciding which among the several available approaches would be most reliable depending on the circumstances (i.e., availability of permanent marks, identifiability of individual tags, knowledge of exact times at liberty, and the various processes affecting the rates of resightings). Appreciable bias may result when methods for estimating tag shedding are applied in situations that differ from those for which they were specifically developed. These results emphasize the need to evaluate the robustness of the estimation procedures before they are applied in novel situations.

## Contributions

LAV: field work, analysis and writing.

AJI: field work.

AMP: analysis and writing.

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## Appendix A.

Assuming that in a double-tagging experiment the daily tag shedding rate  $\lambda$  is constant, tags are indistinguishable and the probability of shedding one tag is independent of the fate of the other, the probability that each tag is retained after  $t$  days,  $k_t$ , is given by  $k_t = \exp(-\lambda t)$  (Chapman et al., 1965), and the probabilities  $P_m$  ( $m = 2, 1, 0$ ) that two, one or zero tags remain attached at time  $t$  since tagging are, respectively:

$$P_2 = (k_t)^2 = \exp(-2\lambda t) \quad (\text{A.1})$$

$$P_1 = 2k_t(1 - k_t) = 2\exp(-\lambda t)[1 - \exp(-\lambda t)] \quad (\text{A.2})$$

$$P_0 = (1 - k_t)^2 = [1 - \exp(-\lambda t)]^2 \quad (\text{A.3})$$

Under these assumptions, the expressions given by Rivalan et al. (2005) for  $Q_{hj}$ , the probability that an individual observed with  $h$  tags in a given occasion retains  $j$  tags at the following resighting,  $N_{hj}$  days later, simplify to:

$$Q_{22} = \exp(-2\lambda N_{22})$$

$$Q_{21} = 2\exp(-\lambda N_{21})[1 - \exp(-\lambda N_{21})]$$

<sup>1</sup> URL: <http://www.nmt.us/products/vie/manual.vie.instructions.pdf> (last accessed: April 2012).

<sup>2</sup> URL: [www.reijns.com/i3s/index.html](http://www.reijns.com/i3s/index.html) (last accessed: April 2012).

**Table A1**

Possible types of individual resighting histories and corresponding likelihoods. Nsa: never seen again. The number 2 in bold indicates that two tags were applied to each individual.

Type of history	Number of recaptures or resightings with:			Example of resighting history	Individual likelihood function $L_i$
	Two tags	One tag	Zero tags		
1	0	0	>0	<b>20</b>	$Q_{20}$
2	0	1	0	<b>21</b> Nsa	$Q_{21}$
3	0	1	>0	<b>210</b>	$Q_{21} Q_{10}$
4	0	>1	0	<b>211</b> Nsa	$Q_{21} Q_{11}$
5	0	>1	>0	<b>2110</b>	$Q_{21} Q_{11} Q_{10}$
6	$\geq 1$	0	0	<b>22</b> Nsa	$Q_{22}$
7	$\geq 1$	0	>0	<b>220</b>	$Q_{22} Q_{20}$
8	$\geq 1$	1	0	<b>221</b> Nsa	$Q_{22} Q_{21}$
9	$\geq 1$	1	>0	<b>2210</b>	$Q_{22} Q_{21} Q_{10}$
10	$\geq 1$	>1	0	<b>2211</b> Nsa	$Q_{22} Q_{21} Q_{11}$
11	$\geq 1$	>1	>0	<b>22110</b>	$Q_{22} Q_{21} Q_{11} Q_{10}$

$$Q_{11} = \exp(-\lambda N_{11})$$

$$Q_{10} = 1 - \exp(-\lambda N_{10})$$

$$Q_{20} = [1 - \exp(-\lambda N_{20})]^2$$

For estimating the probabilities  $Q_{10}$  and  $Q_{20}$  fish must still be identifiable by permanent marks after losing both tags. Depending of the individual's resighting history, the likelihood function of the  $i$ th resighted fish,  $L_i$ , may be one of 11 possible types (Table A1).

When no permanent marks exist, the individual likelihood functions  $L_i$  can only be calculated from different product combinations of  $Q_{22}$ ,  $Q_{21}$  and  $Q_{11}$ . Two alternatives were tested: RIV<sub>nz</sub>, in which all three probabilities were included, and RIV<sub>first</sub>, in which  $Q_{11}$  was excluded.

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