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To catch or to sight? A comparison of demographic parameter estimates obtained from mark-recapture and mark-resight models

K. A. Lee · C. Huveneers · O. Gimenez · V. Peddemors · R. G. Harcourt

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Abstract Accurate assessments of population parameters, such as survival and abundance, are critical for effective wildlife conservation. In order for wildlife managers to undertake long-term monitoring of populations, the data collection must be as cost-effective as possible. Two demographic modelling techniques commonly used are mark-recapture and mark-resight. Mark-resight can be used in conjunction with biotelemetry methods and offers a more cost effective alternative to the traditional mark-recapture models. However, there has been no empirical comparison of the demographic parameters obtained from the two modelling techniques. This study used photographs of natural markings to individually identify wobbegong sharks (*Orectolobus maculatus*) sighted during underwater surveys over a 2 year period, during eight distinct sampling periods, and analysed with Pollock's robust design mark-recapture models. These estimates were then

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K. A. Lee (✉) · V. Peddemors · R. G. Harcourt
Biological Sciences, Macquarie University, North Ryde, Sydney, NSW 2109, Australia
e-mail: kathryn.lee@mq.edu.au

C. Huveneers
Threatened, Endangered, and Protected Species Subprogram, SARDI – Aquatic Sciences, Adelaide, SA, Australia

C. Huveneers
School of Biological Sciences, Flinders University, Adelaide, SA, Australia

O. Gimenez
Centre d'Écologie Fonctionnelle et Évolutive, Campus CNRS, UMR 5175, 1919 Route de Mende, 34293 Montpellier, France

V. Peddemors
Fisheries New South Wales, NSW DPI, Sydney Institute of Marine Science, Sydney, NSW, Australia

compared, using z tests, with Poisson-lognormal mark-resight models that used resightings of sharks previously tagged with telemetry transmitters, and the telemetry data to calculate the number of marked animals present in each sampling period. Sharks were categorised into four groups according to their sex and age-class (adult/juvenile). The results indicated that there was a high degree of transience in the population, with 62 % of sharks only being sighted in one sampling period. Based on normalized Akaike weights, there was no single 'best' model for either type of modelling technique and model averaging was used to determine the demographic estimates. Both models showed higher abundance of wobbegongs in the austral spring and summer seasons, however, the models produced statistically different results for five of the eight sampling periods. The mark-recapture model estimated apparent survival between 78 and 95 %, whereas the mark-resight models estimated it between 48 and 97 %. Crucially, there was no statistical difference between the survival estimates from corresponding sex/age-class. The temporary emigration parameters differed substantially between the model types. The mark-recapture model showed support for Markovian movement, whereas the mark-resight supported random emigration. The timing of the tagging events likely biased the abundance and temporary emigration parameters estimated by mark-resight models and must be taken into consideration when designing a mark-resight study. Despite this, this study shows that robust demographic estimates, that are comparable to labour intensive mark-recapture estimates, can still be obtained using mark-resight methods. Given the substantial increase in biotelemetry studies of medium and large sized vertebrates, mark-resight models may play an important future role in estimating demographic parameters.

Keywords Abundance · Acoustic telemetry · *Orectolobus maculatus* · Photo-identification · Pollock's robust design · Poisson-lognormal mark-resight · Survival · Temporary emigration

Introduction

Estimation and inference on population dynamics is critical for effective wildlife and threatened species conservation. In particular, estimation of demographic parameters is essential in many situations, such as assessing long-term changes in vulnerable populations (e.g. Bradshaw et al. 2007); determining causes of population decline (e.g. Norris 2004); or assessing species persistence under different harvesting pressures (e.g. Servanty et al. 2011) including illegal harvesting (e.g. Mintzer et al. 2013). Methods for collecting demographic data need to be as cost-effective as possible to enable managers to collect long-term datasets, but still yield precise and reliable results.

While the number of modelling techniques available to assess demographic parameters is increasing, two distinct modelling types remain popular: mark-recapture and mark-resight. Mark-recapture models (Otis et al. 1978) involve marking a proportion of the population of interest with individually identifiable marks. 'Marked' animals are then 'captured' in subsequent sampling periods and previously unmarked animals are also 'marked' when captured. Confusingly, mark-recapture models can also be referred to as 'mark-resight models' when previously 'marked' animals are 'recaptured' via sightings. However, in the context of this paper, mark-resight models explicitly refer to models that only require a single marking event and subsequent resighting of both 'marked' and ‘unmarked’ animals are used for estimation (see McClintock and White 2012 for details). Although model assumptions (see Table 1 for summary) may dictate which model is suitable for a particular species or situation, mark-resight models are usually described as both the most cost-effective and as a less invasive alternative to traditional mark-recapture techniques (Minta and Mangel 1989; McClintock and White 2009, 2012). One limitation of the mark-resight models is that it requires the number of ‘marked’ animals in the population at the time of sampling to be known or reliably estimated if animals are not individually identifiable (McClintock and White 2012). However, these models may be readily applied to studies using biotelemetry, such as in habitat use or home-range studies, when demographic information can be obtained while ‘achieving other research objectives’, a main advantage of mark-resight models (Minta and Mangel 1989).

Biotelemetry is widely used to examine ecological questions for terrestrial and marine species (e.g., Cooke et al. 2004; Tomkiewicz et al. 2010; Millspaugh et al. 2012) and can be used to determine the movements of multiple animals over various spatio-temporal scales (Cooke et al. 2004; Hebblewhite and Haydon 2010). However, the high cost of transmitters often only allows a limited number of individuals to be tagged (Cooke et al. 2004; Hebblewhite and Haydon 2010). Potentially, this may decrease the precision and accuracy of the mark-resight models. In this instance, the biases introduced by low sample size could make mark-resight models inadequate and a full mark-recapture study might be necessary to obtain accurate estimates of population abundance and demographic parameters. However, these two methods have not previously been empirically compared in situ. While simulation studies are often employed to evaluate the performance of modelling techniques (e.g. Kendall and Nichols 1995; McClintock and White 2009), these may be unable to mimic the effects on the models that may be introduced by the ecology of the study species or logistical challenges of working in the field.

Therefore, the aim of this study is to compare estimates of abundance, survival, and temporary emigration obtained using mark-recapture (through photo-identification) with those obtained using mark-resight methods (from a combination of telemetry and visual resightings) in a wild elasmobranch population. This was performed using the spotted wobbegong shark (*Orectolobus maculatus*) as a model species because: (1) they have unique natural pigmentation markings that can be used to identify each shark; (2) they can be internally tagged with long-life acoustic transmitters (Huveneers et al. 2006); and (3) they display long-term site fidelity (Carraro and Gladstone 2006; Huveneers et al. 2006), making them suitable for mark-recapture and mark-resight models.

Methods

Study site

The study was undertaken in Cabbage Tree Bay Aquatic Reserve (CTBAR, 33°47′57″S, 151°17′44″E), a small $\sim$0.2 km^2 ‘no-take’ marine reserve off Sydney, Australia (Fig. 1). Habitats within the reserve consist of barren boulders, areas of dense *Ecklonia radiata* and rocky reef covered with macroalgae and sponges, typical to subtidal inshore rocky reefs of temperate, south-eastern Australia (Underwood et al. 1991). There are two distinct reefs within the reserve that are separated by 120 m of sand (Fig. 1).

Table 1 Advantages and disadvantages of mark-recapture and mark-resight models

	Model type	Advantages	Disadvantages
Field methodology			
Use of natural markings and photo-identification	Both mark-recapture and mark-resight	Non-invasive technique Can be sampled from a distance	Marks must be stable for duration of study (Marshall and Pierce 2012) or misidentification estimates must be known to account for marks that may change over time (e.g., scars; Yoshizaki et al. 2009)
	Mark-recapture		Large populations require long-term research efforts due to low recapture rates, impractical for species that are difficult to photograph, or that do not have any distinct markings (Marshall et al. 2011)
	Mark-resight	Individual identifiablity not required for some models (logit-normal estimator and the immigration-emigration logit-normal estimator), but more information is attainable if they are used (McClintock and White 2012)	Can be used where only certain individuals in a population can be individually identified (e.g., Castro and Rosa 2005) and remaining individuals counted as 'unmarked' as long as 'marked' individuals are representative of the population in terms of sighting probability (McClintock and White 2012)
Conventional tagging	Both mark-recapture and mark-resight		Tag attachment may have long-term negative impacts for the animals (e.g., decreased reproductive and survival rates—Froget et al. 1998; Reed et al. 2005)
	Mark-recapture	Diverse range of models can be used	Tag loss can affect population or survival estimates if it is not known or accounted for (Arnason and Mills 1981; Conn et al. 2004) Repeated captures can be costly and labour intensive, or even hazardous for sensitive species (McClintock and White 2007, 2009)

Table 1 continued

	Model type	Advantages	Disadvantages
	Mark-resight	Only a single tagging event therefore more cost, effective and less hazardous for sensitive species (McClintock and White 2007, 2009) Marked individuals seen but not individually identified are still included in the estimates	Animals must be tagged before sightings data can be collected. Animals must be representative of population in terms of sighting probability (McClintock and White 2012) Tags must be field readable for the duration of the study and no tags can be unknowingly lost (McClintock and White 2012)
Model application			
	Both mark-recapture and mark-resight	Animals can be categorised into groups of interest, e.g. by sex and age-class, and model parameters estimated for each group	
	Mark-recapture	Models can include individual covariates, such as total length, for each animal	Encounter history for each animal for each sampling occasion and animals can only be encountered once for each day of sampling
	Mark-resight	If sampling is with replacement then the number of sightings within a closed sampling period can be unlimited (McClintock and White 2012), e.g. no distinction between sampling occasions within secondary sampling periods in Pollock's robust design The exact number of marked animals in the population at the time of sampling is not needed	Marked animals must be individually identifiable. If marked animals are not individually identifiable then sampling is without replacement and each animal can only be sighted once within each distinct, (demographically) closed sampling period and the exact number of marked animals in the population must be known (McClintock and White 2012) Individual covariates, such as total length, can only be modelled for the marked animals

Mark-recapture

Visual surveys

Verification of the use of natural markings and photo-identification to individual identify sharks was assessed prior to sampling (see Supplementary Material). Underwater visual surveys (UVS) were conducted for 10 days (within a 14 day period) every 3 months for over 22 months between January 2009 and November 2010. This resulted in eight primary sampling occasions. Each sampling occasion (January, April, July and October) consisted of 10 secondary sampling days. Each day included two surveys. Surveying consisted of two trained divers following two fixed transects, one along each reef, searching for wobbegongs. The transects were designed to sample a representative proportion of each habitat available within the reserve and to survey areas with expected high and low densities of wobbegongs (Fig. 1d). Upon sighting a wobbegong, photographs of both sides the dorsal and caudal fins (where possible) were taken, and sex, size, and tag number (when applicable) were recorded. Sex was determined by the presence or absence of claspers (Last and Stevens 2009). Total length (TL) of each shark was measured using a tape measure in situ, or estimated if it was not possible to measure the shark due to the terrain. Photographs were matched to individuals taken from previous sampling occasions by eye by two observers and checked by the primary investigator (K.A. Lee).

Mark-recapture model construction

Mark-recapture models were used to estimate population abundance, temporary emigration probability (the probability of an animal temporarily moving in and out of the study area), and survival rates using the Pollock's robust design (Pollock 1982; Kendall and Nichols 1995; Kendall et al. 1997), implemented in the MARK program (version number 6.02; White and Burnham 1999). The robust design assumes an open population between primary sampling periods and a closed population within secondary sampling periods (Pollock et al. 1990; Williams et al. 2002). The primary periods must have sufficient time between them to allow population mixing, while the secondary periods must be within a short enough time period to assume no deaths or births. In addition, temporary emigration is modelled allowing imperfect detection (Kendall et al. 1997). Temporary emigration can be either random, where the absence or presence in a previous sampling period does not determine the 'state' within the next sampling period, or Markovian, where the state in the previous sampling period influences the state in the present.

An encounter history was constructed for each shark captured and photographed for each day of surveying. Sharks were categorised into four groups according to their sex and age class. Sharks were classified as juveniles if they were below minimum length at sexual maturity (115 cm) as reported in Huveneers et al. (2007). All sightings where the sex could not be determined were excluded from the models. To maintain data independence between the two model types, all tagged sharks (see "Mark-resight" section), were excluded from this analysis. The mark-recapture data was analysed using the robust design with Huggins closed capture estimator (Huggins 1989) to allow TL and water temperature to be added as covariates into the model. The model is composed of apparent survival probabilities (ϕ), two temporary emigration probabilities ($\gamma''$and γ'; Kendall and Nichols 1995; Kendall et al. 1997) and the probability of capture (p) and recapture (c). The γ'' parameter is the probability that an animal will remain out of the study area and unavailable for capture in a specific primary sampling period given that the animal was

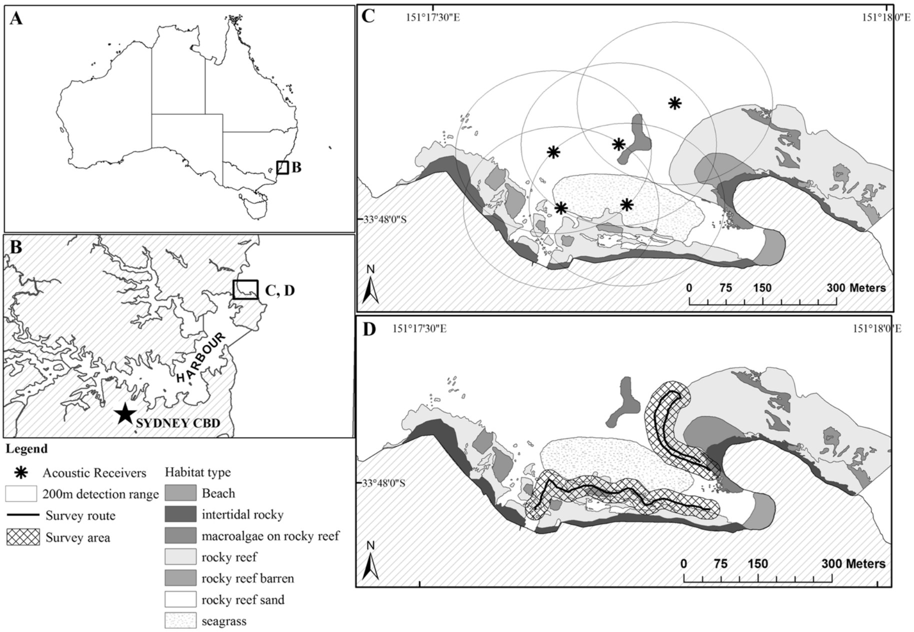

Fig. 1 Map of study site, Cabbage Tree Bay Aquatic Reserve, showing acoustic receiver locations, detection ranges (**c**) and survey transects (**d**)

present in the previous sampling period. The γ' parameter is the probability that an animal will be out of the study area in a specific sampling period given that it was *absent* in the previous sampling period (Kendall and Nichols 1995; Kendall et al. 1997).

Mark-recapture model selection

A set of up to 36 a priori model structures were determined. Apparent survival was tested as time-dependent (ϕ_t), a sex and age interaction (ϕ_g), sex, age and time interaction (ϕ_{gt}), a sex and age interaction with time additive (ϕ_{g+t}), only sex dependent (ϕ_{st}, ϕ_{s+t} *or* ϕ_s), only age dependent (ϕ_{at}, ϕ_{a+t} *or* ϕ_a), or constant (ϕ). Capture and recapture probability were tested using the same parameter effects, with the addition of using TL as an individual covariate, e.g. p_{g*TL}, p_{TL} and p_{g+TL}. Temporary emigration was tested for no movement ($\gamma' = 1$, $\gamma'' = 0$), random ($\gamma' = \gamma''$) or Markovian movement ($\gamma'_{k} = \gamma'_{k-1}$ and $\gamma''_{k} = -\gamma''_{k-1}$). Previous research showed wobbegongs temporarily emigrate from an area (Carraro and Gladstone 2006; Huveneers et al. 2006). However, neither of these studies could evaluate the explanatory variables associated with this movement. Therefore, the effects of fully time-dependent, austral season, breeding/non-breeding season, water temperature, sex, and age-class, as well as interactions between water temperature and sex/age-class were tested on both temporary emigration parameters, e.g. $\gamma''_{g+\text{season}}$, $\gamma''_{g*\text{season}}$ or γ''_{season}. The breeding season of wobbegongs in NSW is December–January (Huveneers et al. 2007), hence both January sampling periods were classified as 'breeding' and the remaining classed as 'non-breeding'. Water temperature was included as a variable in addition to season because there is a lag in the increase/decrease of water temperature and the austral seasons, and wobbegong abundance could be affected by either or both variables.

The step-down approach was used to evaluate each of the parameters in each of these models (Lebreton et al. 1992). The global model was first tested, then keeping the survival and temporary emigration structure general, the 'best' model structure for the capture probabilities was determined using Akaike's Information Criterion adjusted for small sample sizes (AIC_c) and the normalized Akaike weights (Burnham and Anderson 2002). Using this capture probability structure, candidate models with varying temporary emigration were tested using the same methods, and lastly survival. Each model where parameters were suspected to be near the boundary (i.e. the number of reported parameters did not match the number that should be estimated or had unrealistically high or low standard errors) was tested for extrinsic non-identifiability (i.e. an artefact of inadequate data or an estimate near the boundary rather than the model structure itself) using data cloning (Lele et al. 2007). Support for each candidate model was measured using AIC_c differences (ΔAIC_c) where the best model has a ΔAIC_c of zero. Models with ΔAIC_c of less than two from the best model showed substantial support (Burnham and Anderson 2002). Parameter estimates were obtained through model averaging across normalized Akaike's weights, to account for model uncertainty (Burnham and Anderson 2002).

Mark-resight

Acoustic telemetry

Five VR2W acoustic receivers (Vemco Ltd, Nova Scotia, Canada) were deployed within CTBAR up to 160 m apart. Range testing was conducted to determine the effective detection range of the receivers within the reserve (Heupel et al. 2006) and estimated at a minimum of 200 m radius for the worst oceanic conditions. This ensured that the entire protected area was acoustically covered (Fig. 1c). Acoustic receivers were deployed on sand in 6–12 m depth, affixed to a 1.35 m long steel post that was set in a concrete-filled tyre.

Thirteen sharks (five females, eight males) were captured and acoustically tagged within CTBAR. Ten wobbegongs were tagged in June–October (Underwood et al. 1991), and another three in October 2009, 2 weeks prior to the next survey period. Wobbegongs were sampled at random and were caught by diving inside CTBAR using a large hand net (diameter 1 m; mesh size 3 cm) that was held in front of the shark by one diver. A second diver used blunt ended poles (diameter 2 cm; length 1.5 m) to guide the shark into the net. The sharks were brought on board the research vessel and immediately placed in a 200 l tub containing an oxygen-enriched solution of 30 ppm eugenol (AQUI-S, AQUIS-S NZ, Wellington, New Zealand) for anaesthetic induction. Once the sharks were fully anaesthetised, a coded V13-1L acoustic transmitter (battery life ~1,623 days) was inserted into the coelomic cavity using standard surgery practice (see Heupel and Hueter 2001). All sharks were also fitted with an external identification tag, containing a unique number, which was inserted into the musculature below the first dorsal fin.

Mark-resight model construction

The sharks that had been acoustically tagged prior to the UVS were considered as 'marked' and all other sharks were considered 'unmarked'. The mark-resights were based on the 'marked', individually identifiable from their external tags, and 'unmarked' sighted during the UVS. The passive acoustic data was used to determine how many of the 'marked' individuals were present during each sampling occasion. Since the data were collected with replacement and marked individuals were identifiable with permanent field-readable tags, the mark-resight data were analysed using the Poisson-lognormal mark-resight models (McClintock and White 2009). This modelling type also allows the use of Pollock's robust design (using MARK version 6.02; White and Burnham 1999) in a manner analogous to the mark-recapture robust design (Kendall and Nichols 1995; Kendall et al. 1997). The same model grouping structures as the mark-recapture data were constructed (sharks grouped by male/female juvenile/adult), however, individual covariates could only incorporate for the 'marked' individuals. The Poisson-lognormal robust mark-resight model estimates the same survival and temporary emigration probabilities as the mark-recapture models. Individual resighting heterogeneity (σ^2) was set to zero to allow comparison to the mark-recapture models, where no individual heterogeneity in capture/recapture was tested. Abundance (N) was calculated for each primary sampling period by incorporating the number of unmarked animals (U) together with the number of marked, as well as a mean resighting rate (α) for each primary period when individual heterogeneity (σ^2) is equal to zero (McClintock and White 2009).

Mark-resight model selection

The same step-down approach was used for the a priori mark-resight models as the mark-recapture models (see "Mark-recapture model selection" section). However, as the models are sensitive to convergence, initial parameter values estimated from the global model using the sin-link function were provided for each model. If non-convergence was still evident (as indicated by the model output in MARK), the simulated annealing (Goffe et al. 1994) optimisation was used. The 'best' model was determined using the same methods as the mark-recapture models; with the 'best' model structure for the mean resighting rate determined first, then the structure for unmarked animals, then temporary emigration and finally survival. The same model structures were used for survival and temporary emigration as used in the mark-recapture. The main effects used for α were the same used for p and c in the mark-recapture analysis.

Comparison of model types

Apparent survival (ϕ) and temporary emigration (γ'' and γ') estimates from the most parsimonious or the model averaged coefficients from the mark-recapture and mark-resight models were compared using pairwise z tests. Z tests were chosen as they include the standard error into the hypothesis testing thereby accounting for the uncertainty around the estimates. Abundance estimates for each sex/age-class from the mark-recapture model were corrected by the number of tagged sharks sighted in each sampling occasion by dividing the estimates of 'marked' individuals (i.e. those sharks included in the analysis) by the 'marked' proportion of sharks in each occasion (Speakman et al. 2010). The corrected estimates were compared with the mark-resight estimates, which included the tagged and untagged sharks, using pairwise z tests. The total abundance for each primary sampling occasion was calculated by pooling the abundance of each sex/age class from both models. These were then corrected by the number of sharks where the sex could not be determined or photographs could not be taken (and were excluded from the previous analyses) using the methods described above.

Results

Visual surveys

Thirteen sharks were captured and acoustically tagged within CTBAR. Of the sharks tagged between June and October 2008, five were male adults ($\geq$1.15 m), four were female adults ($\geq$1.15 m), and one was a female juvenile (<1.15 m). All three sharks tagged in October 2009 were males, two adults, and one juvenile.

Eighty UVS days over 22 months resulted in 929 encounters with wobbegongs, with only six (0.6 %) of those encounters resulting in no adequate identification photos. On average, 11 sharks were sighted per day (±0.85, range 3–33), with the highest number of wobbegongs recorded in January 2009 (23.1 ± 1.86) and lowest number recorded in April 2009 (4 ± 0.26). A total of 191 sharks were individually identified through photo-identification, including the 13 acoustic tagged sharks. In each primary sampling occasion, there were new sharks that had not been captured previously. No sharks were sighted in every primary occasion. 62 % of sharks were only sighted in a single primary sampling occasion (1 ± 0.07, mode ± SE; Fig. 2), with each sampling including new sharks that had not previously been sighted (Fig. 3).

The mean size of sharks captured during the surveys was 1.25 m TL (range 0.8–1.75 m). 85 % of sharks sighted were adults. 52 % of the sharks identified were male, 38 % were female and 10 % were unable to be sexed.

Demographic parameter estimates

Both the mark-recapture and mark-resight model had the support of multiple models ($\Delta\mathrm{AIC_c} < 7$; Table 2) and were model averaged to obtain parameter estimates. The more complex mark-resight model structures did not converge until the mean resighting rate (α) was constant and the interaction between time and sex/age class had been removed from the unmarked animals (U), emigration parameters, and apparent survival (ϕ).

Mark-recapture models

There was a clear seasonal and annual trend in the abundance estimates from the mark-recapture model, with the highest abundance in summer of 2009 (January 2009) and the lowest in autumns of 2009 and 2010 and the winter of 2009 (Fig. 4a). Total abundance was significantly higher in spring and summer than autumn and winter in both years (Fig. 5). There was no significant difference in the abundance of juvenile males and females in any of the seasons. However, there was a significant difference between all the remaining sex/age-classes in the summer of 2009 and spring of both years and no significant difference in July 2010 (pairwise z tests; Fig. 4a).

The mark-recapture model demonstrated support for Markovian, season-variant temporary emigration (Table 2). There was no model support for temporary emigration being fully time-dependent, nor dependent on breeding season or water temperature ($\Delta\mathrm{AIC_c} > 10$). The probability of a shark emigrating from the study site given they were present in the previous season (γ'') was highest between summer and autumn (January–April; $\gamma'' = 0.91 \pm 0.03$) and lowest between winter and spring (July–October $\gamma'' = 0.56 \pm 0.12$; April–July $\gamma'' = 0.78 \pm 0.12$; October–January $\gamma'' = 0.77 \pm 0.06$). A similar pattern was detected for the probability of a shark remaining an emigrant given it was absent in the previous sampling

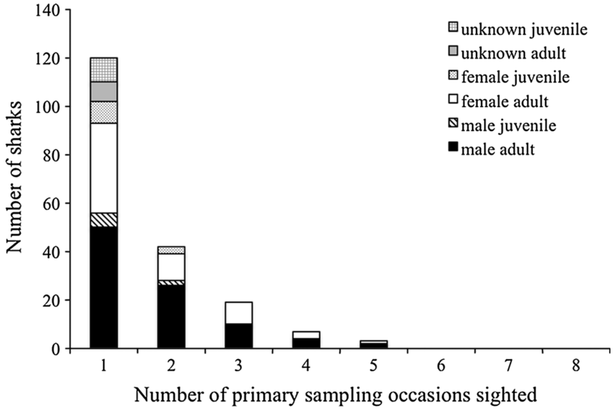

Fig. 2 The number of primary sampling occasions each individually identified wobbegong (*Orectolobus maculatus*), was captured using photo-identification. A season represents a discrete primary sampling period; secondary sampling periods consisted of 10 days of sampling conducted within 14 days every 3 months

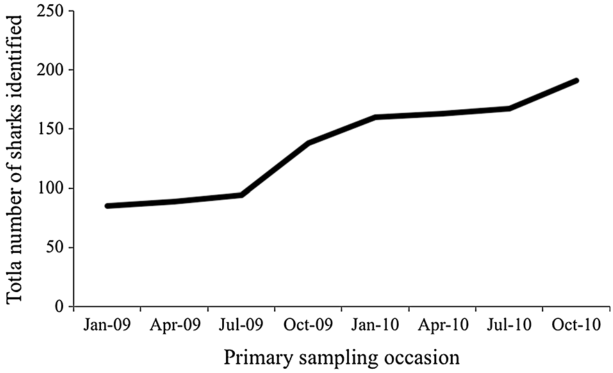

Fig. 3 Discovery curve showing the cumulative number of sharks identified using photo identification. A season represents a discrete primary sampling period; secondary sampling periods consisted of 10 days of sampling conducted within a 14 day period every 3 months

period (γ'), with highest γ' between summer to autumn ($\gamma' = 0.95 \pm 0.03$) and autumn to winter ($\gamma' = 0.87 \pm 0.03$), and the lowest between winter to spring ($\gamma' = 0.54 \pm 0.09$) and spring to summer ($\gamma' = 0.70 \pm 0.12$).

The capture and recapture probabilities were dependent on the age and the TL of the sharks (Table 2). The recapture probability was higher than capture probability for all the sex/age classes. Adult sharks had a higher probability of initial capture than juveniles (adults: $p = 0.17 \pm 0.02$, juveniles: $p = 0.001 \pm 0.01$; z test, p value <0.001). There was, however, no significant difference in recapture probabilities between adults and juveniles (adults: $c = 0.36 \pm 0.01$, juveniles: $c = 0.29 \pm 0.19$; z tests, p value 0.71).

Apparent survival varied by age for the model with the highest AIC_c weighting, but varied by sex/age class, sex only and was constant for the other models contributing to the model averaged estimates (Table 2). Adult males and females had the highest probability

Table 2 The four 'best' model candidates, based on AICc, for mark-recapture and mark-resight models

Model	AIC$_c$	ΔAIC$_c$	AIC weight	Model likelihood	No. para- meters
(i) Mark-recapture					
$\phi(\mathrm{age})\gamma''(\mathrm{season})\gamma'(\mathrm{season})p(\mathrm{age} * \mathrm{TL})c(\mathrm{age} * \mathrm{TL})$	4007.55	0	0.72	1.00	18
$\phi(\mathrm{g})\gamma''(\mathrm{season})\gamma'(\mathrm{season})p(\mathrm{age} * \mathrm{TL})c(\mathrm{age} * \mathrm{TL})$	4010.67	3.11	0.15	0.21	20
$\phi(.)\gamma''(\mathrm{season})\gamma'(\mathrm{season})p(\mathrm{age} * \mathrm{TL})c(\mathrm{age} * \mathrm{TL})$	4011.95	4.40	0.08	0.11	17
$\phi(\mathrm{sex})\gamma''(\mathrm{season})\gamma'(\mathrm{season})p(\mathrm{age} * \mathrm{TL})c(\mathrm{age} * \mathrm{TL})$	4013.17	5.62	0.04	0.06	18
(ii) Mark-resight: no data aggregation					
$\alpha(.)\sigma^2(=0)U(\mathrm{g} + \mathrm{t})\phi(\mathrm{g})\gamma''(.) = \gamma'(.)$	3191.74	0	0.53	1.00	15
$\alpha(.)\sigma^2(=0)U(\mathrm{g} + \mathrm{t})\phi(.)\gamma''(.) = \gamma'(.)$	3192.28	0.55	0.40	0.76	14
$\alpha(.)\sigma^2(=0)U(\mathrm{g} + \mathrm{t})\phi(\mathrm{age})\gamma''(.) = \gamma'(.)$	3195.66	3.92	0.07	0.14	15
$\alpha(.)\sigma^2(=0)U(\mathrm{g} + \mathrm{t})\phi(\mathrm{g} + \mathrm{t})\ \gamma''(.) = \gamma'(.)$	3225.72	33.98	0.00	0.00	23

AICc Akaike information criterion for small samples, *delta AICc* difference in the *AICc* of a model from the minimum *AICc* model, *AICc* weight Akaike weight used in model averaging, ϕ survival, γ'' probability of absence given animal was not present in previous sampling period, γ' probability of absence given animal was present in previous sampling period, *p* capture probability, *c* recapture probability, α mean resighting rate, σ individual heterogeneity (set to 0), *TL* total length, *(.)* an invariant parameter, *t* time-variant parameter, *g* sex and age variant parameter, *sex* sex-variant parameter, *age* age-variant parameter, *season* seasonal-variant parameter, *breed* breeding/non-breeding season-variant

* Indicates an interaction between two parameters

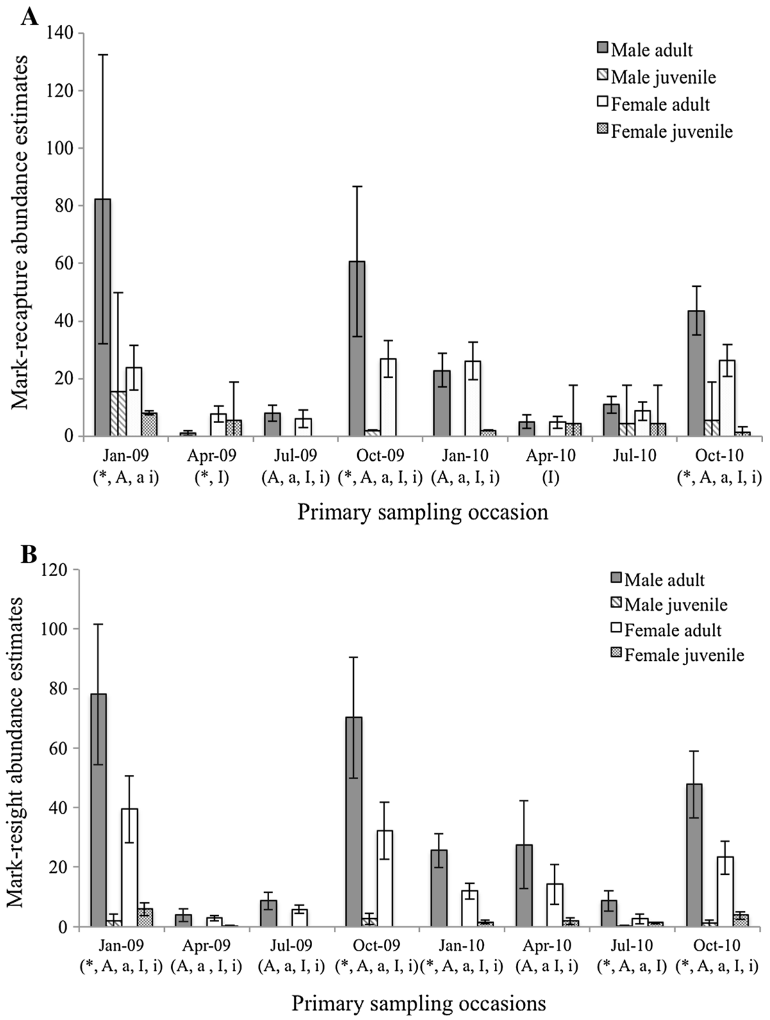

Fig. 4 Mark-recapture (**a**) and mark-resight (**b**) wobbegong abundance estimates. The total abundance estimates have been corrected by to include the sharks that were excluded for the analyses. The Error Bars show the 95 % confidence intervals, which were corrected using the same methods as the total abundance. Pairwise *z* test results: "*, A, a, I, i" indicate a significant difference in the abundance of adult male and females, adult and juvenile males, adult males and juvenile females, adult females and male juveniles and adult and juvenile females, respectively

of survival (both $\phi = 0.95 \pm 0.04$) and juvenile females had the lowest ($\phi = 0.78 \pm 0.11$; juvenile males: $\phi = 0.81 \pm 0.11$). However, there was no significant difference between any of the sex/age classes.

Mark-resight model

The mark-resight model also showed a seasonal and annual trend in abundance (Fig. 4b). There was a higher abundance of adult wobbegongs than juveniles in every primary

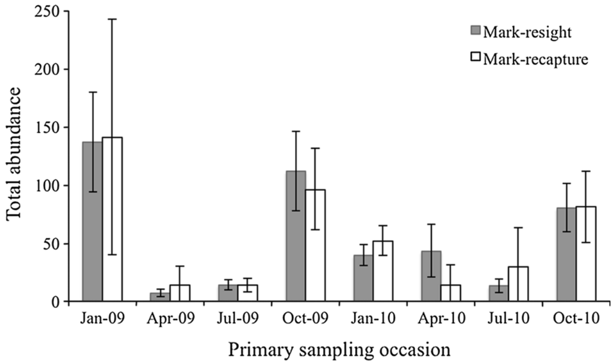

Fig. 5 Total abundance estimates from the mark-recapture and mark-resight model estimates. The estimates have been corrected to include any individuals that were not included in the data analysis. The Error Bars show the 95 % confidence intervals, which were corrected using the same methods as the total abundance

sampling occasion (Fig. 4b). Unlike the mark-recapture model, there was a significant difference in the number of juvenile males and females in every season, except July 2009 when there were no juveniles of either sex present (Fig. 4b). There was a significant difference in adult and juvenile abundance in every sampling occasion (pairwise *z* tests; Fig. 4b).

The mark-resight model showed support for random temporary emigration that was constant between primary sampling periods and sex/age classes ($\gamma = 0.59 \pm 0.09$; Table 2) and a constant mean resighting rate (α; $\alpha = 0.82 \pm 0.20$).

The model with the highest $\mathrm{AIC_c}$ weighting had apparent survival varying by sex and age class, although the model with constant survival also contributed highly to the model averaged coefficients (Table 2). Juvenile females had the highest apparent survival rate ($\phi = 0.99 \pm 0.05$) followed by adult males and females (both $\phi = 0.97 \pm 0.06$), while juvenile males had the lowest survival probability ($\phi = 0.46 \pm 0.40$). However, there was no significant difference between any of the estimates (*z* tests, all *p* values >0.05).

Model comparisons

Total abundance estimates from the mark-resight model were significantly lower in October 2009 and April 2010 than the mark-recapture model and significantly higher in both April 2009, January and July 2010 (Fig. 4a, b). However, there was no significant difference in the estimates between the two modelling techniques for juvenile males (*z* tests, all *p* values >0.05). There was a significant difference for only two primary sampling periods for adult males (autumn, April, of both years: *z* tests, 2009: $p = 0.02$; 2010: $p < 0.001$) and one for juvenile females (spring, October, 2010; *z* test, $p = 0.03$). The abundance estimates for adult females showed higher variation between the two model types, with estimates from only three of the eight sampling occasions showing no significant difference (October 2009 and 2010 and July 2009: *z* tests, *p* values >0.05).

There was no significant difference in the survival rates between the models. However, the γ'' estimated from the mark-resight model was significantly lower in two of the seven estimates (between January–April 2009/2010) than the mark-recapture model. Similarly, the γ' estimated from the mark-resight model was significantly lower in three of the six estimates (between April to July 2009/2010 and January to April 2010).

Discussion

Accurate and reliable estimation of demographic parameters is critical for effective management of wildlife. While simulations to compare model effectiveness is common, this is the first empirical test with free-living wild animals that compares demographic parameters estimated from mark-recapture and mark-resight models. Our results indicate that mark-resight models, based on a small number of animals ‘marked’ with telemetry transmitters and external identification tags and ‘resighted’ with visual surveys, can estimate survival parameters that are not significantly different from those estimated utilising mark-recapture models that require labour intensive photo-identification. Hence, mark-resight models can provide robust data for long-term monitoring using telemetered animals.

However, there are constraints: population abundance and temporary emigration parameters of the mark-resight models may be more susceptible to biases introduced by the timings of tagging events (see “Emigration” section). Lack of convergence in the mark-resight models was likely due to the small number of sharks acoustically tagged. This issue is inherent to the cost and other technological limitations associated with using acoustic telemetry to mark individuals (Cooke et al. 2004; Hebblewhite and Haydon 2010). Therefore, while mark-resight models appear robust enough to calculate similar survival estimates to mark-recapture models, they lose the power to detect finer-scale population differences, such as variation between sexes or ages, when the number of tagged animals is limited. Accordingly, adopting mark-resight designs are likely to have constraints that need to be carefully considered when designing long-term and/or large-scale studies.

Derived patterns of abundance of wobbegongs

All the models tested show clear seasonal trends in abundance of wobbegongs. Abundance was highest during the austral summer and lowest during winter. The mark-recapture analyses showed new sharks were sighted throughout the study period but with a high degree of transience. 62 % of sharks were only sighted within a single primary sampling occasion and new sharks were sighted throughout the study. But, the acoustic telemetry data also showed that there were tagged sharks present within the study area, which were not sighted during the visual surveys. This suggests that the wobbegong sharks sighted within the study area are likely to be part of a larger population and that the abundance estimates in this study should be used an indicator of the minimum population size for the local area.

Seasonal breeding aggregations have been observed in several other shark species (e.g. *Stegostoma fasciatum*: Dudgeon et al. 2009; *Carcharhinus melanopterus, C. amblyrhynchos, Negaprion acutidens* and *Triaenodon obesus*: Speed et al. 2011). In this study, the abundance of adult wobbegongs was higher than juveniles, which could indicate that sharks are aggregating to reproduce. This is supported by wobbegong abundance peaking during the breeding season (December–January—Huveneers et al. 2007). However, when temporary emigration based on breeding season was incorporated into the model, model selection indicated that austral season (summer, winter, autumn, and spring) was a better explanatory variable than breeding season. This may be due to the length of the study in relation to the triennial reproduction cycle of spotted wobbegongs (Huveneers et al. 2007) and a longer study period may be needed to detect differences between the austral and breeding/non-breeding seasons. Alternatively, the aggregations observed may be related to increased prey availability (Taylor 1996; Heyman et al. 2001). Analysis of oceanographic conditions within the region of the study site shows an increase in nutrient-rich waters during the summer months (Suthers et al. 2011). However, further research would be needed to quantify if this resulted in increased prey and wobbegong abundance.

Emigration

All the mark-recapture models indicated the probability of an animal emigrating was dependent on its state, present or absent, in the previous sampling period (Markovian movement). However, despite no statistical difference between the temporary emigration parameters, the mark-resight model indicated random movement out of the study site. This could be a result of the sharks being acoustically tagged during the winter/spring months when the probability of them emigrating out of the study site before the next season was the lowest, thereby increasing the probability that the animals would be present during the summer months and biasing the model. Three additional sharks were acoustically tagged a couple of weeks before the commencement of the October 2009 surveying season. This likely biased the model for the next sampling period and may account for why the mark-resight model had higher abundance estimates than the other models in October 2009. These results highlight that it is very important to consider the timing of the marking periods for the mark-resight models.

Capture, recapture and mean resighting estimates

The mean resighting rate from the mark-resight model was higher than the recapture rates from the mark-recapture model, even though a number of the tagged sharks were present in the study area and not sighted during the surveys. A sympatric species of wobbegongs, the ornate wobbegong (*Orectolobus ornatus*), displays a high degree of fine-scale site fidelity (Carraro and Gladstone 2006; Huveneers et al. 2006). If site fidelity of the spotted wobbegong is similar, it would increase the likelihood of recapturing the same individuals, explaining the higher resighting rate capture probability than recapture probability obtained from the mark-recapture model. The timing of the tagging events in 2009 may have also increased the likelihood of resighting those tagged individuals. Both of these issues should be taken into account when designing mark-recapture and mark-resight models. Random stratified sampling methods should be used to ensure all areas within the study site are sampled and the behaviour of the focus species should be taken into account when considering the timing of tagging events for mark-resight models.

The mark-recapture model showed that adults had a higher capture and recapture probability than juveniles. Wobbegongs prefer areas with high topographic complexity and crevice volume (Carraro and Gladstone 2006). Therefore, the size of the shark may have biased the ability to see the sharks during the surveys as the smaller juveniles may have been occupying small cervices. Adult wobbegong may also display greater site fidelity than the juveniles because the latter may have to move around until they find uninhabited space to occupy. The mark-resight model resighting rates for the juvenile sharks may have been biased by the low sample size (one shark for each of the sexes). This is reflected in the low precision of the resighting rate for juvenile male. Therefore, the sample size of each of cohorts of interest, e.g. sex or age, should be taken into consideration when employing mark-resight models.

Survival estimates

Apparent survival estimates calculated from the mark-recapture in this study were high for all age-classes (78–95 %). Survival was estimated as even higher by the mark-resight model for adults and juvenile females (97 and 99 %, respectively), although there was no statistical difference with the mark-recapture model. There are no previous estimates for apparent survival of spotted wobbegongs to compare these estimates to. However, the estimates obtained for the adults were higher than those estimates for other shark species with similar ecology, such as zebra sharks (*Stegostoma fasciatum*, survival = 0.88 and 0.87 for males and females respectively; Dudgeon et al. 2008), or for larger pelagic shark species, such as whale sharks (*Rhincodon typus*; annual survival 0.73–0.89, Bradshaw et al. 2007; annual survival 0.34–0.78, Rowat et al. 2009).

Once again, the timing of the tagging events for the mark-resight model likely biased the model to estimate apparent survival, as the sharks tagged were more likely to remain in the area. The mark-resight model also estimated the apparent survival as highest and lowest for juvenile females and males, respectively. However, given that only a single juvenile of each sex was tagged, the model may have been biased to produce imprecise apparent survival estimates. This reiterates the importance of considering the timing of the tagging/marking events for mark-resight models and ensuring individuals from all sex/age-classes of interest are marked/tagged.

This study was conducted within a no-take reserve that was declared a marine protected area due to the high species diversity (DECCW NSW 2010), including wobbegong sharks. Therefore, this area may provide a refuge for at least a proportion of the sharks, and so reflect higher survival rates than populations in areas open to fishing. The temporary emigration, however, showed that the sharks emigrated from the site in at least a couple of the sampling occasions and that the CTBAR population comprises mainly transient sharks, with the majority only captured once. Although the longevity of wobbegongs is unknown, they are slow growing (Huveneers et al. 2013) and only reproduce every 3 years (Huveneers et al. 2007), and are therefore likely have long life spans like many other shark species (Last and Stevens 2009). This, together with the high level of transience of the population, suggests that small marine reserves are unlikely to contribute significantly to the long-term conservation of wobbegong sharks. At the same time, the high apparent survival rates suggest that the harvesting pressures on this population are currently low. Stringent management regulations introduced in 2008 reducing the total catch of all wobbegong species in New South Wales (NSW), may therefore be contributing to the recovery of this localised population. Longer-term mark-recapture studies on vulnerable wobbegong populations outside of marine reserves, and over a larger spatial and temporal scale would be needed to fully assess the adequacy of the new regulations.

Near-shore, seasonal aggregations have been reported for a number of elasmobranch species using surveying or mark-recapture techniques (e.g. Taylor 1996; Dudgeon et al. 2008; Marshall et al. 2011). This can have important implications for both potential harvesting and/or management of near-shore fisheries that could negatively impact the shark populations. Accurate demographic estimates are needed to assess long-term population changes (e.g. Bradshaw et al. 2007) in order to ensure potential anthropogenic impacts are adequately addressed. Mark-resight models could play an important role in determining long-term monitoring of such populations, especially now that acoustic transmitters routinely have battery lives of up to 10 years thus allowing monitoring of populations over a larger temporal scale than previously possible.

Conclusion

In this study we have shown how mark-recapture and mark-resight approaches can provide robust estimates with utility for management. We have shown that it is possible to obtain abundance and survival estimates from mark-resight models even where the sample size of individuals tagged with telemetry devices is relatively small. If differences between biological groups, such as sex or age-classes, are of interest, the number of animals tagged must incorporate adequate sampling of each grouping of interest. The highest quality biological information will be obtained if marking is undertaken in a way that accounts for seasonal patterns of emigration, thereby minimising bias in temporary emigration parameters. This suggests that marking of individuals should account for seasonal movements, if possible, to reduce bias of any models. Given that biotelemetry is increasingly used for investigations of long-range movements and conservation ecology, it is clear that using this technology to develop mark-resight models has the potential to enormously add value to ecological studies.

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