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Integrating acoustic telemetry into mark–recapture models to improve the precision of apparent survival and abundance estimates

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Abstract Capture–mark–recapture models are useful tools for estimating demographic parameters but often result in low precision when recapture rates are low. Low recapture rates are typical in many study systems including fishing-based studies. Incorporating auxiliary data into the models can improve precision and in some cases enable parameter estimation. Here, we present a novel application of acoustic telemetry for the estimation of apparent survival and abundance within capture–mark–recapture analysis using open population models. Our case study is based on simultaneously collecting longline fishing and acoustic telemetry data for a large mobile apex predator, the broadnose sevengill shark (*Notorhynchus cepedianus*), at a coastal site in Tasmania, Australia. Cormack–Jolly–Seber models showed that longline data alone had very low recapture rates while acoustic telemetry data for the same time period resulted in at least tenfold higher recapture rates. The apparent survival estimates were similar for the two datasets but the acoustic telemetry data showed much greater precision and enabled apparent survival parameter estimation for one dataset, which was inestimable using fishing data alone. Combined acoustic telemetry and longline data were incorporated into Jolly–Seber models using a Monte Carlo simulation approach. Abundance estimates were comparable to those with longline data only; however, the inclusion of acoustic telemetry data increased precision in the estimates. We conclude that acoustic telemetry is a useful tool for incorporating in capture–mark–recapture studies in the marine environment. Future studies should consider the application of acoustic telemetry within this framework when setting up the study design and sampling program.

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Introduction

Estimates of demographic parameters such as abundance and survival are integral to effective wildlife conservation and management (Sollman et al. 2013). Capture–mark–recapture (CMR) models are popular tools for estimating a suite of demographic parameters (Williams et al. 2002). In CMR models, individual animals are captured and tagged, released and then either subsequently recaptured once (e.g. dead recovery) or multiple times. Low capture probabilities, i.e. the probability that an individual animal is captured on a given sampling occasion, can result in imprecise or biased estimates (Pine et al. 2003). Low recaptures may be typical in studies of rare or threatened species, or species that are difficult to access (Sollman et al. 2013). The use of multiple data sources can increase precision of demographic parameter estimates (e.g. Burnham 1993; Powell et al. 2000; Schaub et al. 2007), and in some cases permit the estimates of additional parameters (Kendall et al. 2013).

Telemetry or biologging data has been used as auxiliary data in CMR studies in terrestrial and freshwater systems (e.g. Powell et al. 2000), but is only starting to be incorporated in these types of studies in marine systems. Primarily, auxiliary telemetry data has provided information on survival, temporary emigration and location during non-capture periods, and more recently for informing abundance estimates (Pollock et al. 2004; Bird et al. 2014; Eveson et al. 2012). For example, Johnson et al. (2010) incorporated multiple data sources including radio-telemetry and mark–resight data into Bayesian state–space models to estimate abundance and other demographic parameters for Sierra Nevada bighorn sheep *Ovis canadensis sierra*. Bird et al. (2014) utilised radio-telemetry data to inform temporary emigration within mark–recapture models for estimating abundance in a freshwater population of trout cod *Maccullochella macquariensis*.

In the marine environment, where there is very high attenuation of radio waves, acoustic telemetry is becoming a widespread tool with greater coordination (e.g. Ocean Tracking Network; Cooke et al. 2012), reduced cost and miniaturisation of tags (Cooke et al. 2004). The research applications for acoustic telemetry are diverse spanning areas of ecology, physiology, evolution and theoretical physics (Payne et al. 2014). However, applications of acoustic telemetry to estimating demographic parameters are currently limited, with some focus on natural mortality in fish and shark species (e.g. Heupel and Simpfendorfer 2002; Knip et al. 2012; Whitlock et al. 2012). More recently, Lee et al. (2014) incorporated acoustic telemetry within a mark–resight framework to estimate abundance of wobbegong sharks (*Orectolobus maculatus*).

Here we present a novel application of acoustic telemetry for the estimation of apparent survival and absolute abundance within a mark–recapture analysis. Our case study is based on simultaneously collecting CMR data from research longline fishing and acoustic telemetry data for a large mobile apex predator, the broadnose sevengill shark (*Notorhynchus cepedianus*) at a coastal site in Tasmania, Australia. *Notorynchus cepedianus* occur in high numbers in coastal Tasmania over the warmer months (spring–autumn) where they exert significant predation pressure on prey inhabiting these areas (Barnett et al. 2010a, c; Barnett and Semmens 2012), and likely play a crucial role as one of the key apex predators in temperate waters. Information on absolute abundance will give a greater understanding of their effects and influence on ecosystem structure and dynamics when they aggregate at foraging sites over the warmer months.

Traditional CMR analysis on longline fishing data can yield highly uncertain population estimates or inestimable parameters due to low recapture rates (e.g. Hewitt et al. 2010; Dale et al. 2011). Specifically, we utilise open population models and compare estimates of apparent survival from acoustic telemetry data with longline fishing data, as well as assess how incorporating acoustic telemetry data into mark–recapture analyses of longline fishing data affects the estimates of absolute abundance. Given the increasing acoustic telemetry infrastructure and applications to diverse fields of research, we anticipate that developing methods to incorporate acoustic telemetry data into mark–recapture studies will be beneficial to estimating demographic parameters for ecological, conservation and management purposes.

Materials and methods

The field component of this study was conducted in Norfolk Bay, south-east Tasmania, Australia. Norfolk Bay is a relatively shallow (average depth 15 m; maximum depth 20 m) semi-enclosed bay with an area of approximately 180 km^2 (Fig. 1). Fishing and acoustic telemetry methods, protocols, site maps and receiver locations are described in Barnett et al. (2010c, 2011). Briefly, seasonal longline sampling was conducted at four fixed sites in Norfolk Bay from summer 2006–2007 to summer 2008–2009. Sampling took place for a minimum of four nights per season, with four longlines set at each of the fixed sites per night. Longlines consisted of 210-m lead-core mainline (8 mm diameter), with 1-m stainless steel snoods and 50 hooks per line. Soak times were typically 4 h, with longlines set between 0100 and 0200 hours and hauling beginning at

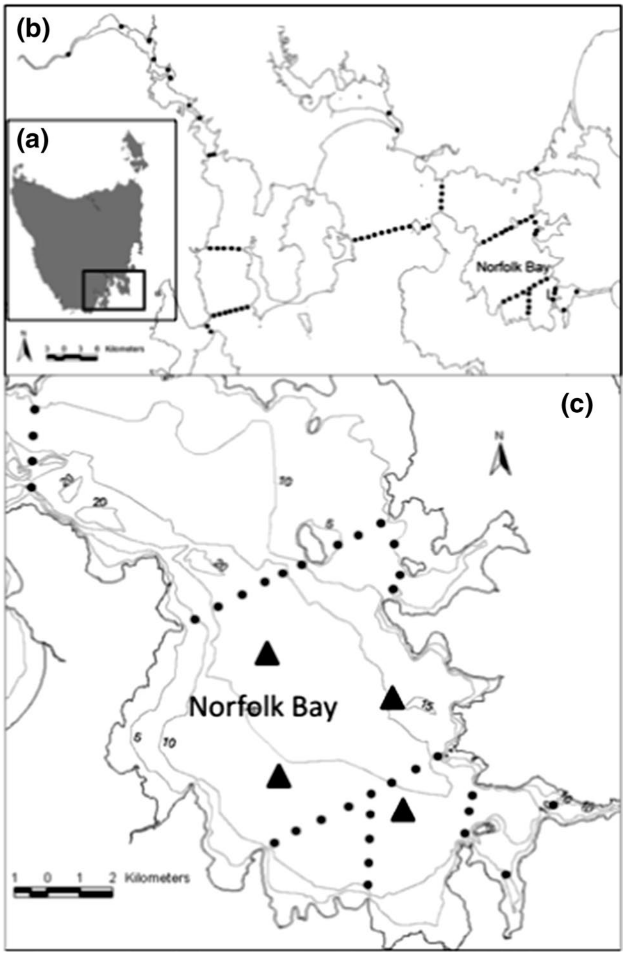

Fig. 1 Tasmania (*a*) showing Norfolk Bay and the Derwent Estuaries (*b*). The location of the four longline fishing locations (*filled triangle*) and the acoustic telemetry receivers (*filled circle*) in Norfolk Bay which were used for this study are shown (*c*)

sunrise (0500–0600 hours). Sharks were measured to the nearest cm total length, sexed and tagged in the dorsal fin with plastic Jumbo tags (Dalton, UK) and released.

An array of 33 acoustic receivers was deployed in Norfolk Bay (VR2 receivers; VEMCO, Halifax, Canada) to determine the residency of *N. cepedianus* fitted with acoustic transmitters in the Bay. Individually-coded V16 acoustic transmitters (VEMCO; two models used with battery life of over 2 years and over 5 years) were implanted into the body cavity of 25 *N. cepedianus* via a 1- to 2-cm incision in the abdominal wall. Twenty sharks were tagged between December 2007 and March 2008 and an additional five sharks between 17 October and 19 November 2008. Sharks ranged in size from 153 to 284 cm total length (TL); see Barnett et al. (2010b, 2011) for details of individuals tagged. Range testing of the acoustic receivers demonstrated a 100 % detection rate within a radius of 400–500 m. The receivers were position approximately 800 m apart in the curtains to enable complete coverage of sharks entering and exiting the study area (Barnett et al. 2011).

Acoustic data analysis

The daily occurrence of acoustically tracked *N. cepedianus* in Norfolk Bay from January 2008 to the end of May 2009 was plotted to provide a visually interpretable timeline of residency (Fig. 2). A residency index was calculated as the ratio between the number of days an animal was present in Norfolk Bay to the number of days from the first to the last detection, with a value of 1 indicating it was detected every day and 0 indicating it was never detected. Since *N. cepedianus* generally exit Norfolk Bay for winter, the residency index was calculated for two periods, prior

Fig. 2 Timeline showing the days that each acoustically tagged *Notorhynchos cepedianus* ($n = 25$) occurred in Norfolk Bay as recorded by acoustic receivers from January 2008 to June 2009. The winter months June–September, between the two main sampling seasons are shown with *shading*

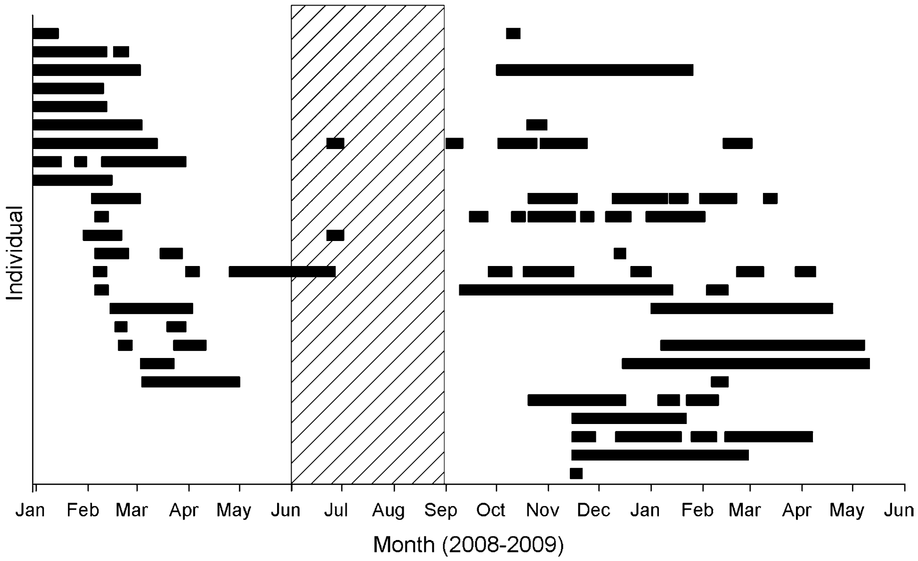

Table 1 Encounter history dates and intervals showing numbers of marked and recaptured individuals for the longline and acoustic data

Year	Acoustic tagging	Month year	Fishing date(s) in month	Longline		Acoustic	
				# Marked	# Recaptures	# Marked	# Recaptures
1	.	Dec 2006	4	36	–		
1	.	Jan 2007	14	17	1		
1	.	Feb 2007	13	9	0		
1	.	Mar 2007	18,19	24	1		
1	.	Apr 2007	25	2	0		
1	.	May 2007	12	1	0		
2	.	Sep 2007	22	4	0		
2	.	Oct 2007	5	5	0		
2	.	Oct 2007	31	10	0		
2	.	Nov 2007	9, 12	19	1		
2	A	Dec 2007	4	3	0	2	–
2	A	Jan 2008	2	8	0	7	0
2	A	Jan 2008	30	3	0	1	8
2	A	Feb 2008	9	19	1	4	8
2	A	Feb 2008	17, 21, 22	32	2[a]	3	8
2	A	Mar 2008	7, 12	9	1	1	3
2	A	Apr 2008	7	7	1	0	2
2	A	May 2008	15	5	0	0	1
2	A	May 2008	31	5	4	0	1
3	A	Oct 2008	11	11	2	0	4
3	A	Oct 2008	23, 24	2	1	1	6
3	A	Nov 2008	18, 19	5	3[a]	4	4
3	A	Dec 2008	11	4	0	0	6
3	A	Jan 2009	10	17	2	0	8
3	A	Jan 2009	19	2	1	0	6
3	A	Jan 2009	31	3	0	0	4
3	A	Feb 2009	13	2	0	0	6

[a] Two sampling periods when an acoustically-tagged shark was recaptured by longline fishing

to winter (January 2008–June 2008) and after winter (September 2008 onwards). Every time *N. cepedianus* individuals entered Norfolk Bay, the number of consecutive days each individual resided was calculated and divided by the total visits by all sharks to gain an average residency time (in days) per visit.

Mark–recapture analyses

Data preparation

The occurrence of *N. cepedianus* across each continuous spring and autumn period are classified as a sampling year. Longline sampling occurred during the warmer months over 3 years and acoustic telemetry studies were run concurrently to the longline sampling for part of the second year and the entirety of the third year (Table 1).

Mark–recapture analysis for separate longline fishing and acoustic data

Mark–recapture analyses were implemented on the longline and acoustic data to estimate apparent survival and abundance parameters spanning the total sampling duration (3 years for longline-only data and 2 years for combined longline and acoustic telemetry data) as well as investigating years separately. Encounter histories were constructed for each data type. These were comprised of presence/absence data for tagged individual sharks for a given sampling period. Sampling periods were pooled over 1–3 fishing days and a value of 1 was given if a shark was caught and/or detected during that time (present) or a value of 0 was given if a shark not caught or detected (absent). Sampling periods were spaced between 2 and 4 weeks apart (see Table 1 for dates). For the longline fishing data, encounter histories were constructed for four sampling durations: (i) the entire 3-year longline study, (ii) years 2 and 3 combined, (iii) year 2 only and (iv) year 3 only. The first year of longline fishing was not investigated separately as this did not have concurrent acoustic sampling. For sampling durations (ii), (iii) and (iv), only the dates within year 2 that were concurrent with the acoustic sampling were included. All the year 3 sampling periods were concurrent with the acoustic sampling. The acoustic telemetry data were subsampled to generate encounter histories that matched the sampling frequency of the corresponding longline fishing days for the sampling durations (ii), (iii) and (iv).

Open population models were used for analysis as the study site was not closed to migration between years and is also not likely to be closed within years. In general, *Notorynchus cepedianus* leave Norfolk Bay for winter and return in spring (Barnett et al. 2010a, 2011; Stehfest et al. 2014), and, although they reside in the bay from spring to autumn, individuals move in and out of the bay over this time (see "Results" and Fig. 1).

Cormack-Jolly-Seber (CJS) open populations models (Cormack 1964; Jolly 1965; Seber 1965), which estimate apparent survival (φ) (i.e. animals that survive and do not permanently emigrate from the population) and recapture probabilities (p) between each sampling period, were run on the longline and acoustic telemetry encounter histories separately for each of the durations (denoted by the superscripts $^{\mathrm{LL}}$ for longline data and $^{\mathrm{AT}}$ for acoustic telemetry data). CJS models do not require information on the unmarked individuals captured at each sampling event for parameter estimation. In particular, for the acoustic telemetry data it is not possible to know how many untagged animals may be in the receiving range of the VR2W receivers during the sampling period. Therefore, CJS models were used to compare the φ estimates between the different data types. For each sampling duration and data type, four models were assessed where φ and p were considered constant over time (.) or were allowed to vary with monthly sampling intervals (t) as defined in Table 1. The analyses were implemented using the CJS option with the default sin link function in Program MARK version 6.2 (White and Burnham 1999).

To estimate population abundance, Jolly–Seber (JS) open mark–recapture models (Jolly 1965; Seber 1965) were constructed for the longline data for all four of the sampling durations using the POPAN option in Program MARK version 6.2 (Schwarz and Arnason 1996; White and Burnham 1999). As JS models do require information on the unmarked individuals captured at each sampling event to estimate abundance these models cannot be implemented on the acoustic telemetry data alone. JS models were constructed using time variant (t) and constant periods (.) for apparent survival (φ), recapture probability (p) and entry probability (β). To eliminate any confounding in the time variant models from parameter products, the first and last recapture probability values were constrained at the value of the adjacent time period [i.e. $p(1) = p(2)$; $p(k) = p(k - 1)$] (Schwarz and Arnason 1996). JS models that only allow for losses (Pollock et al. 1990), i.e. all permanent migration occurs prior to sampling, were also implemented. The notation $\beta(0)$ is used to represent these models as all β parameters are restricted to 0 within the analyses. The models were fitted using the logit link function for φ and p, the log function for N and the multinomial logit link function for β to constrain the set of parameters to $\beta \leq 1$ (White and Burnham 1999) Model selection was based on Akaike's Information Criterion for small sample sizes (AIC$_{\mathrm{c}}$) (Burnham and Anderson 2002).

Combined acoustic and longline Monte Carlo mark–recapture analysis

The CJS analyses conducted on the longline and acoustic data separately generated similar φ estimates for corresponding durations. However the longline data φ^{LL} estimates had very high uncertainty (CV range from 4.32 to 31.4 %) with very low recapture probabilities ($p < 0.05$). To reduce the effect of this high uncertainty on abundance (N) estimates, we devised a combined acoustic and longline mark–recapture analysis approach for estimating abundance. Initially, φ estimates were generated for each time period using a CJS modelling approach whereby the acoustic telemetry data and the longline fishing data were incorporated into the same analysis as two separate groups (denoted as $\varphi^{\mathrm{combined}}$). The resulting $\varphi^{\mathrm{combined}}$ estimates were then incorporated into JS models to estimate N^{combined} through a Monte Carlo simulation procedure. Firstly, the mean and SE for the estimated $\varphi^{\mathrm{combined}}$ values were used to derive the α and β parameters of a beta distribution for 1000 samples (a continuous distribution defined on the interval [0, 1]). Next, φ was drawn randomly from this distribution and used as a fixed parameter in the JS analysis for the corresponding longline fishing sampling duration, using the most parsimonious model as identified by the initial longline JS analysis. This process was repeated 1000 times to build posterior distributions and capture estimation uncertainty. We used the program R v.2.13.0 (R Development Core Team 2011) package RMark v.2.1.3 (Laake and Rexstad 2008) to construct the model and simulation loops for program MARK v.6.2 (White and Burnham 1999). For sampling duration (iii) year 2 only, the inclusion of the longline data in the CJS analysis resulted in much lower φ values than for the other time period ($\varphi^{\mathrm{combined}} = 0.7595$, CV $= 7.6$ %). Given that this $\varphi^{\mathrm{combined}}$ estimate is much lower than for the other time periods as well as the CJS φ^{AT} for same time period (year 2 only), there is likely to

Table 2 Apparent survival (φ) estimates based on CJS analyses of the longline fishing and acoustic data separately and then combined as two groups within a single analysis

Time series	Longline		Acoustic		Acoustic and longline	
	φ^{LL}	CV (%)	φ^{AT}	CV (%)	$\varphi^{combined}$	CV (%)
(i) 3 years	0.8740*	4.32	–			
(ii) Years 2 and 3	0.9011*	8.0	0.9214**	2.3	0.9332***	2.1
(iii) Year 2 only	NA[a]		0.9098**	7.5	0.7595***	7.6
(iv) Year 3 only	0.9838*	31.4	0.8548*	5.9	0.8587***	5.6

CJS models used to generate the estimates based on AIC$_c$ ranking: *$\varphi(.)\ p(.)$, **$\varphi(.)\ p(t)$, ***$\varphi(.)\ p(g)$

[a] φ inestimable

be downward bias due to the sparse longline data. Therefore, the Monte Carlo simulation procedure was conducted on this time period using the CJS φ estimates from the acoustic telemetry data alone ($\varphi^{AT} = 0.9098$, CV = 7.5 %; Table 2).

Assumptions for open mark–recapture models

Firstly, the population is assumed to be open to births, deaths, emigration and immigration between sampling periods. While little is known about the reproduction and mortality of wild *N. cepedianus*, the population in Norfolk Bay appears to be open to emigration and immigration, as each year sharks are tracked through the acoustic telemetry receiver networks leaving Norfolk Bay for winter and returning the following spring/summer (Barnett et al. 2011). During their seasonal visits, acoustic telemetry receivers in Norfolk Bay and neighbouring Derwent River locations show that acoustically-tagged *N. cepedianus* move in and out of Norfolk Bay (~8 months, October–May), spending an average of 25 days in the bay per visit. (Barnett et al. 2011; Stehfest et al. 2014). Sex-biased differences in movement have been discerned from telemetry data (Stehfest et al. 2014), but there does not appear to be any consistent within-season movement among individuals (see Fig. 2). Movement may result in biased parameter estimates from CJS and JS models due to temporary emigration effects within the analysis (Kendall et al. 1997). However, if temporary emigration is random, then the bias will be minimal. For Markovian temporary emigration, the direction of bias will depend on the specific temporary emigration parameter values. The collected data preclude modeling that enables the estimation of these parameters in this case. Secondly, sampling is assumed to be instantaneous relative to the sampling interval and releases are made immediately following the sample. This assumption is met, as sampling was conducted in a single day or pooled over a couple of close days relative to the weeks or months between the sampling trips. Third, the marks are unique and are not lost or overlooked with time. The marks are unique in that conventional fishery tags are individually numbered and the acoustic tags emit a unique code. There was no evidence of tag loss from acoustic tags as these were surgically inserted. However, fishery tags were lost from four animals, evident by the tagging scar when they were recaptured. This is the equivalent to 16 % tag loss based on the recapture of 25 individuals in total. Therefore, the loss of some tags could lead to a slight overestimation in abundance and underestimation of survival. Fourth, all marked individuals have the same probability of survival (all individuals for JS models and only marked individuals for CJS models). Available information implies this would be the case for *N. cepedianus* using Norfolk Bay, where, as well as in the coastal areas of Tasmania in general, natural mortality is likely to be very low. Neonates and small juveniles were not caught in coastal habitats (Barnett et al. 2010c), and mortality rates tend to be low for adult sharks as most predation occurs at the smaller juvenile stages (e.g. Heupel and Simpfendorfer 2002; Cortés 2004; Dudgeon et al. 2008). In coastal areas of Tasmania, *N. cepedianus* are the apex predators, and there are no consistent threats of predation. Cannibalism would be the most plausible source of mortality from predation, but dietary analyses suggest this is naturally low in Norfolk Bay (Barnett et al. 2010b). Evidence from previous studies in this area suggest that *N. cepedianus* should have minimal post-release mortality after tagging, e.g. overall 15 % recapture rate (relatively high for sharks) and 100 % survivorship of animals tagged with acoustic tags in Tasmania (Barnett et al. 2010c, 2011). Between seasons, when *N. cepedianus* leave coastal protected areas, there is the risk of animals being caught by fisheries. In a movement study, 2 out of 43 acoustically tagged individuals were caught in fisheries (Barnett et al. 2011). And fifth, all individuals have the same probability of capture (Pollock et al. 1990). It was not possible to control for heterogeneity of capture in this study. However, as all sharks caught in Norfolk Bay were of a large size, i.e. the catch consists of adults and sub-adults, with no neonates or small juveniles (Barnett et al. 2010c), differences in capture probabilities due to size variation were reduced.

Capture differences between longline fishing and acoustic telemetry methods were addressed by separating these data into two groups.

Results

Mark–recapture

A total of 263 *N. cepedianus* were tagged with conventional tags in Norfolk Bay, from which 29 were recaptured (overall 11 % recapture rate). Two of the 89 *N. cepedianus* tagged in the first year were recaptured in the same year. In the second year, an additional 124 individuals were tagged and 14 of the 213 tagged sharks recaptured. An additional 50 individuals were tagged in the third year and 13 of the total 263 tagged sharks were recaptured. Daily recaptures were low with the majority having only 1 recapture per longline session and up to 4 on one occasion (Table 1).

Acoustic monitoring

Notorynchus cepedianus rarely occurred in Norfolk Bay throughout winter, but during the warmer months residency varied from 2 to 111 consecutive days, with an average residency of 25 days per visit (Fig. 2). Residency index ranged from 0.23 to 1, averaging 0.84. Following the initial two sampling days that sharks were tagged with acoustic tags (4 December 2007 and 2 January 2008), 1 to 8 acoustically tagged sharks were detected (i.e. recaptured) by receivers on subsequent longline sampling days, resulting in a total of 75 recaptures by receivers, with an average of 5 per longline sampling day (Table 1). Two of the acoustically tagged sharks were also recaptured by longline sampling on one occasion each (Table 1).

Mark–recapture modelling

CJS apparent survival estimates

The AIC model ranking supported models with constant apparent survival estimates [i.e. $\varphi(.)$]. Recapture probability for longline data supported models with $p(.)$, acoustic data models supported both $p(t)$ and $p(.)$ depending on the sampling duration; and the combined two-group models support $p(.)$ (Table 2; ESM 1). Recapture probabilities for the longline data were very low ($p < 0.03$) for all sampling durations. Conversely, the recapture probabilities for the acoustic telemetry data were much higher with estimates at least tenfold greater (i.e. $p > 0.30$ for all sampling durations, combined and separate acoustic telemetry data) than for the longline data (Fig. 3). The CJS φ estimates were all high ($\varphi > 0.8548$) and similar between the longline fishing and acoustic telemetry data sets, except for sampling duration (iii) year 2 only, where φ^{LL} could not be estimated away from the upper boundary of 1 with longline fishing data. The combined acoustic and longline φ estimate for year 2 only ($\varphi^{\mathrm{combined}} = 0.7595$, CV $= 7.6$ %) was considerably lower than for the acoustic data alone (φ 0.9098^{AT}, CV $= 7.5$ %). For the other time periods φ estimates ranged between $\varphi^{\mathrm{AT}} = 0.8548$ (year 3 only acoustic data) to $\varphi^{\mathrm{LL}} = 0.9838$ (year 3 only longline data). The variation around the φ estimates was narrow for the models including acoustic telemetry data (all CVs ≤ 7.6 %). Similarly low CVs were found for the larger longline data sets for sampling duration (i) all 3 years and (ii) years 2 and 3 (CV ≤ 8 %). However, the CVs were much higher when considering longline data for duration (iv) year 3 (CV $= 31.4$ %) separately (Table 2).

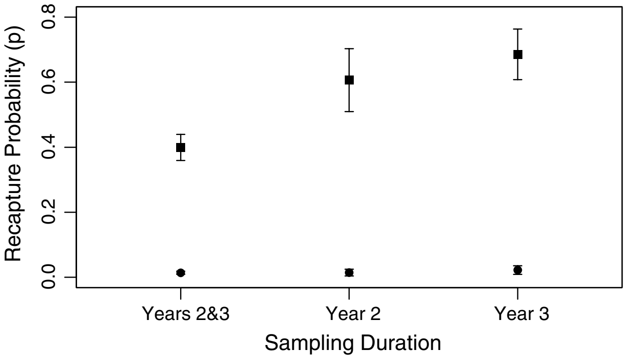

Fig. 3 CJS recapture probability estimates (p) and SE values for *Notorhynchos cepedianus* from the longline sampling data (*filled circle*) and the combined longline and acoustic telemetry data (*filled square*). Values for the three combined sampling durations are shown: (ii) years 2 and 3, (iii) year 2 only, and (iv) year 3 only

JS abundance estimates

For all the sampling periods, the most parsimonious model had the model structure $\varphi(.)$ $p(t)$ $\beta(0)$ N (ESM 2). The recapture probability estimates that varied over time were low with mean values for all time periods <0.1 and most <0.05. POPAN models with $\varphi(t)$ were not supported as the φ parameters were inestimable for several of the periods. Likewise, $\beta(t)$ was not supported in the POPAN models as many of the β parameters estimates were not discernable from 0 and models with $\beta(.)$ had inestimable parameters. The abundance estimates for the longline fishing data only and the combined acoustic and longline data were similar for the corresponding sampling durations (ii) and (iv). However, estimation precision was considerably different between the two approaches. For the longline fishing data only, the CVs for all sampling durations ranged 38.0–54.7 %. Conversely, the CVs based on the distribution of N

Table 3 Abundance (*N*) estimates based on (1) longline data only and (2) combined acoustic and longline data

Sampling duration	1. Longline data only		2. Combined acoustic and longline data	
	N^{LL} (mean)	CV (%)	N^{combined} (median)	CV (%)
(i) 3 years[a]	3700.35	38.0	–	
(ii) Years 2 and 3[a]	1088.52	49.5	1130.01	12.2
(iii) Year 2[a]	977.30	48.0	1246.00	34.3[b]
(iv) Year 3[a]	438.49	54.7	562.25	12.7

[a] Model is $\varphi(.)\ p(t)\ \beta(0)$; $\varphi(.)\ p(.)\ \beta(0)$

[b] Estimate is based on $\varphi^{\mathrm{AT}} = 0.9098$, CV = 7.5 %

values generated from the Monte Carlo JS analyses for the simulated data using the CJS $\varphi^{\mathrm{combined}}$ estimates were much smaller, ranging from 12.2 to 12.7 % (Table 3; Fig. 4). For sampling period (iii) year 2 only, the CJS φ^{AT} from the acoustic data alone was used to inform the JS model. The resulting N^{combined} estimates and precisions were similar to those for the sampling duration (ii) years 2 and 3 combined ($N^{\mathrm{combined}} = 1246$); however, the CV (34.3 %) was considerably larger than for the other sampling durations.

Discussion

Estimating demographic parameters in wildlife population is challenging. These challenges are amplified in fishing data where recapture rates are typically low in large water bodies, including many freshwater and most marine systems (Hewitt et al. 2010), and as demonstrated for longline fishing in this study. Only 2 of the 25 acoustically tagged sharks were recaptured on longlines, despite up to 8 sharks being recorded on acoustic receivers during a single fishing period and, therefore, presumably present and available for capture on longline sampling nights. This suggests low catchability for the longline fishing gear used. Possible reasons for this low catch include: sharks caught once are wary of baits; sharks present may have already fed prior to baits being deployed; or individuals that were detected on the acoustic receiver array may have not moved close enough to be attracted to the baited line. *Notorynchus cepedianus* have been recorded swimming over 30 km in a night (Barnett et al. 2010b) and prefer the deeper sections of Norfolk Bay (Barnett and Semmens 2012). The fixed longline sites were all in deeper waters and spread over a large section of the bay (Barnett et al. 2010c), suggesting that sharks had a good chance of detecting baits. Alternatively, the high abundance of elasmobranchs in the bay (this study; Barnett and Semmens 2012) means competition could limit access to bait. Indeed, when retrieving longlines in warmer months, the vast majority of hooks had either caught an elasmobranch or the bait was removed without hooking the animal (Barnett and Semmens 2012; Barnett et al. 2010c).

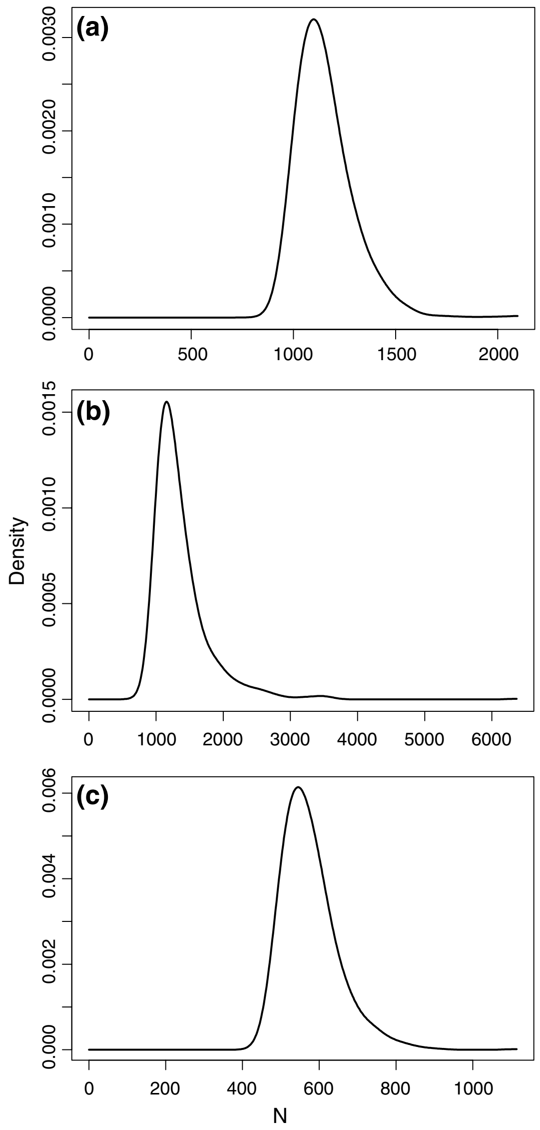

Fig. 4 Density plots of simulated abundance values for *Notorhynchos cepedianus*, **a** years 2 and 3 combined, **b** year 2 only (apparent survival, φ, from acoustic telemetry alone incorporated into the JS model), and **c** year 3 only (both models including φ generated from the combined acoustic telemetry and mark–recapture CJS analyses)

Low recapture rates are problematic as they tend to lead to low precision in estimates and require more restrictive models, which reduces the capacity of these tools for detecting population trends, diagnosing causes of population declines and directing management options (Johnson et al. 2010). The use of multiple data types can assist in increasing the precision in analyses (Burnham 1993), and here we show that incorporating acoustic telemetry into CMR analyses of longline fishing data increases the precision for apparent survival and abundance estimates. Furthermore, acoustic telemetry data has enabled estimation of apparent survival for one of the sampling durations (year 2 only), which was not estimable with the longline data only.

There was concordance between the apparent survival estimates and error margins from the longline and acoustic telemetry data for sampling durations (ii) and (iv) using the CJS models. However, the acoustic telemetry data showed much higher precision alone, and when combined with the longline data, than the longline data separately. In the case of duration (iv) year 3 only, the CV showed a very large reduction from 31.4 % for the longline data to only 5.6 % for the combined analyses. This agrees with previous studies demonstrating increased precision in CMR estimates from combining multiple data types (e.g. Besbeas et al. 2002; Schaub et al. 2007). Furthermore, Johnson et al. (2010) showed that, when the estimates from data types resulted in different values, the results obtained from the combined model generally are weighted towards the data providing the higher precision. This was found with the results from duration (iv) where the φ estimates from the combined data analyses were much more similar to the acoustic telemetry data only than the longline data only (Table 2).

For duration (iii) year 2 only, the acoustic data enabled φ to be estimated where the longline data alone for this interval were unable to generate estimates away from the upper boundary. This is likely due to the particularly low recapture probabilities in this sampling duration. The φ estimates from the acoustic telemetry data alone were similar to those for other sampling durations demonstrating the utility of acoustic telemetry data for CJS models. Conversely, the φ estimate using the combined datasets for this duration, (iii) year 2 only, was considerably lower than for all other CJS analyses. The lower estimate may be a result of temporary emigration, which is not measured in the CJS analyses. However, given the higher φ estimates from the acoustic telemetry data alone for this duration, as well the higher φ estimates from the other durations, the combined φ estimate is more likely to be demonstrating negative bias due to the low recapture probabilities in the longline data.

It is not possible to use acoustic telemetry data alone in JS models as it does not allow for unmarked animals, which are required for estimating abundance. However, we were successfully able to increase the precision in the abundance estimates of the JS models by incorporating the CJS φ estimates generated from the combined acoustic telemetry and longline data into the JS analysis through a Monte Carlo simulation process. Furthermore, there was good concordance of abundance estimates between the JS analyses on the longline data only and the JS Monte Carlo simulations. In contrast, for sampling duration (iii) year 2 only, incorporating the acoustic telemetry φ estimates into the JS model did not result in a substantial increase in precision (see Table 3). Therefore, when recapture rates are extremely low, including auxiliary data may only marginally improve the precision.

The approach employed here utilised simple open population models (CJS and JS) as well as existing software (Program MARK and RMark) in a two-step analysis process. It is possible to write down the joint likelihood of the two data types, which is just the product of the two independent likelihoods. Maximum likelihood estimates could be obtained from this likelihood in one step but requires the development of specialized software, whereas our two-step approach uses the existing software. Based on the joint likelihood, Bayesian estimates could also be developed. Bayesian methods are now being very widely used in capture–recapture models (e.g. Poole 2002; Dupuis and Schwarz 2007). The acoustic telemetry data were also useful for validating the use of open population models for this study system by tracking the movement of individual sharks away from the study site (see Barnett et al. 2011; Stehfest et al. 2014). One major benefit of the proposed analytical approach here is its simplicity and accessibility to applied users. However, the approach is limited to the use of open population models, as well as using simplified models where φ estimates have been kept constant over time. In this case, time-constant φ was supported by AIC model selection; however, different approaches would need to be assessed to account for φ varying with time. The apparent survival parameters estimates from the CJS and JS models do not separate out the effects of permanent emigration from true survival. However, depending on the study system, these estimates can still be informative. In particular, large elasmobranchs tend to have low mortality (e.g. Cortés 2004; Smith et al. 1998) and, therefore, high estimates of apparent survival are likely to approach true survival. For juvenile elasmobranchs where mortality is higher, CJS models may supplement other methods for estimating survival from acoustic telemetry data such as Kaplan–Meier estimates (e.g. Heupel and Simpfendorfer 2002; Pollock et al. 1989).

CJS and JS models estimate a limited number of parameters and do not account for many other confounding factors such as temporary emigration and individual heterogeneity. For example, temporary emigration can negatively bias survival estimates and inflate abundance estimates (Kendall et al. 1997). More complex models such as the Robust Design (Pollock et al. 1990) include temporary emigration as well as other parameters of interest, but also present extra mathematical challenges for incorporating biotelemetry presence/absence data. Recent interest in abundance estimation has also focused on mark–resight models (Arnason et al. 1991; Neal et al. 1993; White and

Shenk 2001; McClintock and White 2009, 2012). Unlike CMR models, animals are only captured and tagged once and then subsequently observed and not recaptured. Potentially mark–resight can be less invasive and expensive than traditional CMR (McClintock and White 2012; Sollman et al. 2013). Biotelemetry data can readily be incorporated into mark–resight models such as has been demonstrated in recent studies (Lee et al. 2014; Sollman et al. 2013). However, mark–resight is not applicable to all situations. Broadnose sevengill sharks do not surface, and underwater observations are not possible in Norfolk Bay for resighting events. Similar limitations exist for permanently submerged animals in low-visibility habitats such as estuarine and river systems, as well as for dispersed animals, which are difficult to observe without capture. In these circumstances, CMR approaches may be more applicable.

CMR approaches are useful for obtaining estimates of absolute abundance, which have application in managing exploited species, conservation planning for threatened species and assessing the influence of predators on prey species (Forcada et al. 2009; Sharples et al. 2009; Kirkwood et al. 2010; Gwinn et al. 2011). In this case study, *N. cepedianus* are apex predators that likely play an important role in Norfolk Bay, which is an important nursery habitat for commercially important gummy shark and over-exploited school sharks. Dietary analyses show that *N. cepedianus* are a major predator for these species (Braccini 2008; Barnett et al. 2010a) and, therefore, abundance estimates will enable a greater understanding of natural mortality for prey species with further downstream application.

Due to the difficulties associated with estimating abundance and other demographic parameters in the marine environment, the continual development of integrating technologies such as biotelemetry into mark–recapture frameworks is important. In particular, acoustic telemetry is a rapidly increasing field and is often associated with corresponding mark–recapture studies through fishing or visual surveys. However, challenges with low recapture rates in mark–recapture studies are not restricted to marine environments and are common to those for rare and threatened species in freshwater and terrestrial environments. Stationary acoustic telemetry systems were first developed for the marine environment but have been routinely adopted within freshwater systems (Cooke et al. 2013). In terrestrial environments, the first automated telemetry systems were established with VHF receiver stations monitoring radio-collared animals (Cochran and Lord 1963). Radio-telemetry data have been incorporated into a CMR framework to inform demographic parameters such as a study combining radio-telemetry with physical banding mark–recapture monitoring on Greater Sage Grouse over a 10-year period (Gibson et al. 2013). For rare and elusive species such as tigers and other wild carnivores, GPS collar technology, which enables the continuous monitoring of collared animals (Tomkiewicz et al. 2010), could be subsampled in a similar way to acoustic telemetry data to account for the presence or absence of individuals within the mark–recapture study area. CMR data may be visual surveys or obtained by camera traps, which are increasingly being used to obtain population estimates including for wild carnivores such as ocelots and tigers (Trolle and Kéry 2003; Trolliet et al. 2014). Camera trap CMR data could be supplemented with GPS collar data using the analytical method we proposed here or other models as suggested above.

Incorporating telemetry data into mark–recapture frameworks will benefit future CMR studies for wildlife populations with low recapture potential, and, in many cases, allow smaller sample sizes to be used in mark–recapture models. Crucially, it is important to be aware of this potential application of telemetry prior to data collection and to design field sampling regimes appropriately to get the most out of this immensely useful data. Future research should also focus on incorporating acoustic telemetry into the development of more complex models that will enable greater parameterization and flexibility.

Author contribution statement A.B. originally formulated the idea. C.L.D. and A.B. developed the concept. A.B. conducted the fieldwork. C.L.D., M.B. and K.P. developed and conducted the analyses. C.L.D. and A.B. wrote the manuscript; J.S., M.B. and K.P. provided editorial advice.

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