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Applying the multistate capture–recapture robust design to characterize metapopulation structure

Delphine B. H. Chabanne*,[1], **Kenneth H. Pollock**[1,2], **Hugh Finn**[1,3] **and Lars Bejder**[1]

[1]Cetacean Research Unit, School of Veterinary and Life Sciences, Murdoch University, Murdoch, WA 6150, Australia; [2]Department of Applied Ecology, North Carolina State University, Raleigh, NC 27695-7617, USA; and [3]Curtin Law School, Curtin University, Bentley, WA 6102, Australia

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Summary

1. Population structure must be considered when developing mark–recapture (MR) study designs as the sampling of individuals from multiple populations (or subpopulations) may increase heterogeneity in individual capture probability. Conversely, the use of an appropriate MR study design which accommodates heterogeneity associated with capture occasion varying covariates due to animals moving between 'states' (i.e. geographic sites) can provide insight into how animals are distributed in a particular environment and the status and connectivity of subpopulations.

2. The multistate closed robust design (MSCRD) was chosen to investigate: (i) the demographic parameters of Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) subpopulations in coastal and estuarine waters of Perth, Western Australia; and (ii) how they are related to each other in a metapopulation. Using 4 years of year-round photo-identification surveys across three geographic sites, we accounted for heterogeneity of capture probability based on how individuals distributed themselves across geographic sites and characterized the status of subpopulations based on their abundance, survival and interconnection.

3. MSCRD models highlighted high heterogeneity in capture probabilities and demographic parameters between sites. High capture probabilities, high survival and constant abundances described a subpopulation with high fidelity in an estuary. In contrast, low captures, permanent and temporary emigration and fluctuating abundances suggested transient use and low fidelity in an open coastline site.

4. Estimates of transition probabilities also varied between sites, with estuarine dolphins visiting sheltered coastal embayments more regularly than coastal dolphins visited the estuary, highlighting some dynamics within the metapopulation.

5. *Synthesis and applications*. To date, bottlenose dolphin studies using mark–recapture approach have focussed on investigating single subpopulations. Here, in a heterogeneous coastal–estuarine environment, we demonstrated that spatially structured bottlenose dolphin subpopulations contained distinct suites of individuals and differed in size, demographics and connectivity. Such insights into the dynamics of a metapopulation can assist in local-scale species conservation. The MSCRD approach is applicable to species/populations consisting of recognizable individuals and is particularly useful for characterizing wildlife subpopulations that vary in their vulnerability to human activities, climate change or invasive species.

Key-words: distribution, heterogeneity, local transitions, mark–recapture, spatial scales, subpopulations, wildlife conservation

Introduction

At an individual level, wildlife tends to be neither uniformly nor randomly distributed across land- or sea-scapes but to occur in association with particular environmental features (Legendre & Fortin 1989). At a population-level, species are typically distributed in a series of populations or 'subpopulations', as in a metapopulation model (i.e. set of spatially separated populations of the same species which interact at some level, Levins 1969). Emigration and immigration between subpopulations may occur through either permanent additions or subtractions or only the short-term presence or absence of individuals (Brown *et al.* 2016; Sprogis *et al.* 2016). Individuals within a population (or subpopulation) may have ranging patterns that overlap or are connected with a particular locality (Sprogis *et al.* 2015).

Such population structure must be considered when developing mark–recapture (MR) study designs because the sampling of individuals from multiple populations (or subpopulations) may increase heterogeneity in individual capture probability (Brown *et al.* 2016). Conversely, it is feasible

*Correspondence author. E-mail: d.chabanne@murdoch.edu.au

for an appropriate MR study design also to provide insight into how animals are distributed in a particular environment and the status and connectivity of any subpopulations that are present (Brooks & Pollock 2014).

Since its development in the late 1800s (Petersen 1895), the MR approach has been widely used for assessing wildlife abundance, distribution and demographic processes. Here, we attempted to use extensions of a MR study design, the multistate closed robust design (MSCRD), to investigate demographic parameters and connectivity between putative subpopulations that were spatially predefined in a heterogeneous coastal and estuarine environment.

In MR studies, individual-specific encounter ('capture') histories may be used to generate capture probabilities, and to estimate apparent survival rates (i.e. the true survival and permanent emigration combined) and abundance (i.e. number of animals using the study area, Lettink & Armstrong 2003). The underlying assumption of homogeneity in individual capture probabilities is often violated because of practical constraints on sampling (see review by Lindberg 2012). Heterogeneity in individual capture probability may be reduced by the inclusion of time-dependent covariates (e.g. year), individual time-constant covariates (e.g. sex) and covariates associated with individual capture occasion (e.g. weight, social affiliations, geographical locations: Pollock *et al.* 1990).

The closed robust design (CRD) was built using two different temporal scales: (i) two or more open sampling occasions (hereafter 'primary periods') in which the time interval between periods is sufficiently long enough to allow for births and immigration, and for losses from deaths and emigration; and, (ii) closed sampling occasions (hereafter 'secondary occasions') set within each of the primary periods and where the intervals between occasions are sufficiently short so that no gains and losses are assumed to occur (Pollock 1982). By sampling across multiple temporal scales, CRD models estimate temporary emigration (TE) and immigration between primary periods as well as abundance and apparent survival parameters without having to assume equal probability of capture over the entire study period (Kendall & Pollock 1992; Smith *et al.* 2013). Thus, biases due to heterogeneity in capture probability are minimized and abundance and apparent survival are estimated from multiple occasions allowing better precision (Kendall 1990). The incorporation of time-constant covariates (e.g. sex) within the CRD models also has advantages in reducing the heterogeneity in capture probability and estimating abundance and apparent survival specific to covariate classes (e.g. males, females).

Another MR study design, the multistate mark–recapture (MS) approach, enables the use of fixed set of categorical 'states' that are discrete covariates measured upon capture of the individual, e.g. geographic location, reproductive state (e.g. Hestbeck, Nichols & Malecki 1991; Cam *et al.* 2004). Like time-constant covariates, an advantage of including categorical 'states' in MS models is a homogeneity assumption that is state specific and the ability of the models to provide state-specific estimates for abundance and apparent survival (Lindberg 2012). As well as modelling immigration and emigration to and from an unobservable state (i.e. outside the study area, and thus part of the apparent survival estimates), MS models have a unique feature in which transition among 'states' can be estimated (Darroch 1961; Arnason 1972, 1973). The transition between states is the probability that an individual, alive and in the state x, just before $t + 1$, emigrates into the state y. Transition between states may be either temporary or permanent and both contribute to the estimate of transition probability.

Here, we applied the MSCRD approach with 'states' referring to geographic sites (see 'site' hereafter), which utilizes aspects of MS models and the CRD (Nichols & Coffman 1999) (Fig. 1) for several reasons. Firstly, the MSCRD allows for greater flexibility in model specifications for individual heterogeneity in capture probability. Critically, heterogeneity can be modelled according to: (i) individual-level characteristics (i.e. a time-constant covariate such as sex), (ii) individual-level responses to capture (i.e. state measured upon capture) or (iii) the relevant temporal scale for captures (primary periods vs. secondary occasions). Secondly, the MSCRD can provide abundance estimates for each 'state' within each primary period. Finally, the inclusion of multiple secondary occasions within each primary period increases the capture probability, which improves the precision of the apparent survival estimates and transition probabilities (White, Kendall & Barker 2006; Lindberg 2012).

Our aim is to show how the MSCRD, with its innate flexibility in modelling heterogeneity in capture probabilities, can simultaneously provide demographic parameter estimates for multiple putative subpopulations associated with particular sites as well as describe their conservation status and connectivity to other subpopulations. This approach allows for use of: (i) capture probabilities to affirm (or refute) the putative grouping of individuals associated with a particular site as a distinct 'subpopulation' (i.e. homogeneity within sites); (ii) estimates of the variation in abundance (i.e. primary period changes in the number of individuals in any geographic site) and apparent survival (i.e. the probability of surviving and staying in any site) to assess the occupancy (or residency) of a group of individuals in that site; and (iii) transition probabilities between sites to describe the interconnectivity of those groupings.

Previous MSCRD studies using site as a 'state' have generally had other aims and applications: e.g. detecting changes in transition probabilities before, during and after an environmental perturbation affecting one state (see O'Connell-Goode, Lowe & Clark 2014) or human development activities (see Brooks & Pollock 2014); evaluating individual fitness over time (see Gibson *et al.* 2014) or quantifying the connectivity (i.e. transition of individuals) between areas exposed to different management regimes (see Lee 2015). Notably, this study aimed to examine the dynamics, status and connectivity of multiple putative subpopulations each associated with a particular site.

To pursue the above aim, we applied the MSCRD approach in a mark–recapture study of Indo-Pacific bottlenose dolphins *Tursiops aduncus* ('dolphin' hereafter) in coastal and estuarine waters near Perth, Western Australia. We defined the geographic sites based on the coastal geography and landforms and the known presence of small resident subpopulations in an

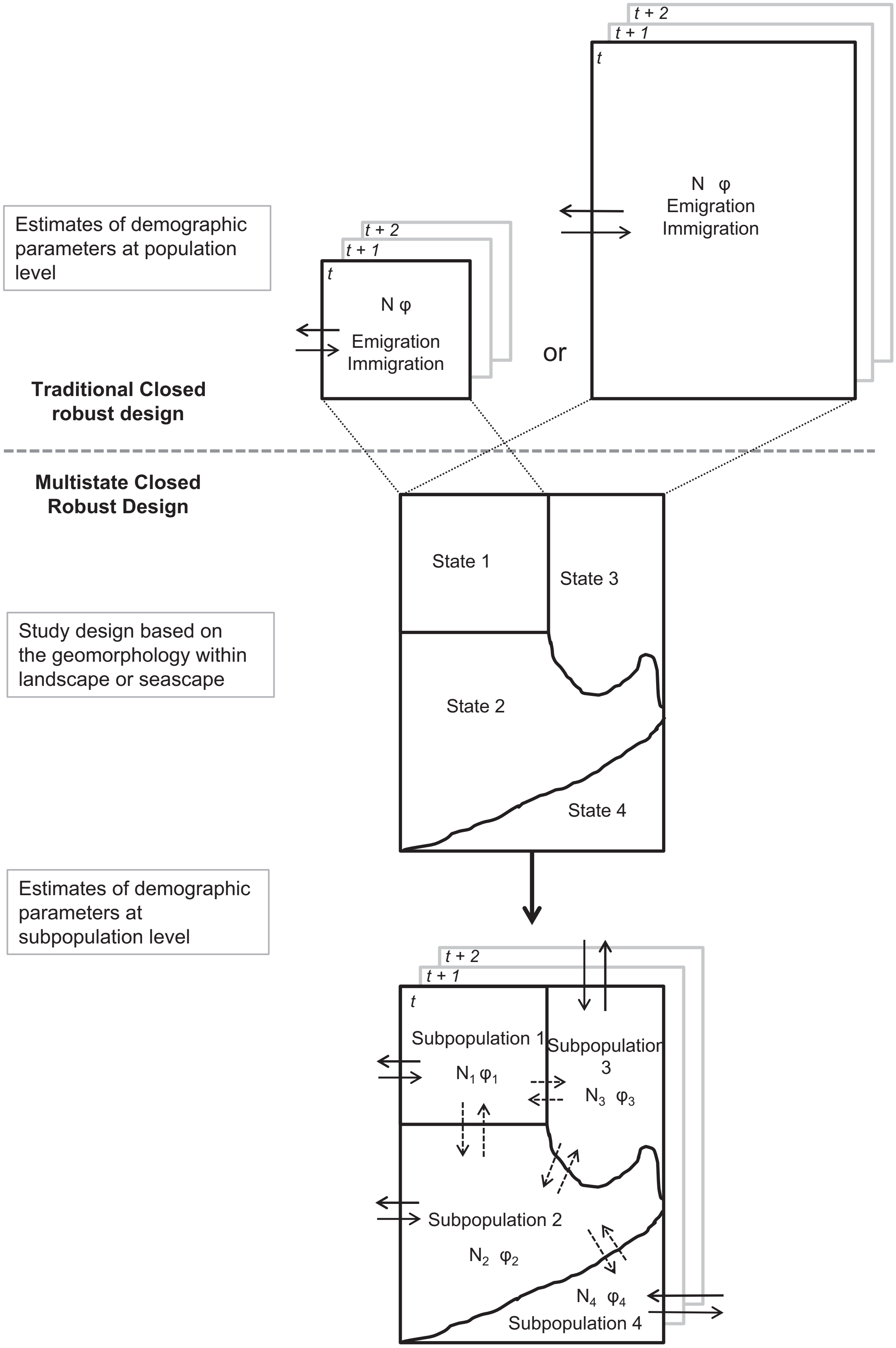

Fig. 1. Traditional closed robust design (CRD) vs. multistate closed robust design (MSCRD) approaches to characterize metapopulation structure and dynamics through demographic parameters. Both approaches allow estimation of abundance (*N*), apparent survival rate (φ) and emigration and immigration [solid arrows] either time varying (*t*, *t* + 1, *t* + 2, etc.) or constant. In addition, MSCRD models estimate any transition probabilities ψ [dashed arrows] between subpopulations associated with states (i.e. geographic sites).

estuary ($N \approx 20$, Chabanne *et al.* 2012) and a nearby coastal embayment ($N \approx 75$, Finn 2005) (but without knowledge of their connectivity to each other, or to other potential subpopulations in the study area).

We then used individual capture histories obtained from 4 years of year-round boat-based photo-identification surveys to estimate: (i) capture probabilities per site to evaluate and compare the occupancy pattern of dolphins within sites (i.e. to explore heterogeneity between sites); (ii) apparent survival rates and abundances so as to verify putative site-related groupings through the assessment of site fidelity (i.e. close to true survival, stable abundances) and (iii) transition probabilities so as to characterize movement between site-related groupings (i.e. the metapopulation dynamic).

Materials and methods

FIELD METHODS

Study area and field sampling design

Our study area encompassed an area of 275 km^2, extending for 45 km along the coast of Perth and then inland to include the Swan Canning Riverpark (SCR), an estuarine reserve of about 55 km^2 (Fig. 2). Three sites were defined based on coastal geography, principal landforms (estuary, open waters and coastal embayment) and information from previous local studies (Waples 1997; Finn 2005; Chabanne *et al.* 2012): (i) the estuary (SCR) and two sites in coastal waters, (b) Gage Roads (GR), a length of open coastline with mostly sandy beaches and small areas of rocky reef and seagrass, and (c) Cockburn Sound/Owen Anchorage (CS/OA), a semi-enclosed embayment. The northern section of the embayment (OA) is of <10 m depth, except in a shipping channel (max depth: 14·7 m), with substrates mainly of shell-sand and seagrass. The southern section (CS) has shallow (<10 m) margins, a deep (~20 m) central basin, and seagrass, sand, silt and limestone substrates. In comparison to GR, CS/OA experiences intensive industrial and recreational use, with threats to dolphins including entanglement and illegal feeding (Finn 2005; Donaldson, Finn & Calver 2010), industrial and harbour development (Finn 2005) and shell-sand dredging (BMT Oceania 2014). For practical reasons (i.e. wind and sea conditions), CS and OA were split and run as two separate sub-sites, although there were jointly sampled in 84% of the secondary occasions (see below).

Between June 2011 and May 2015, we collected year-round mark–recapture data for individual dolphins using boat-based photo-identification surveys following predefined transect routes (Fig. 2). While the same transect route was conducted in the estuary (due to the confined waters), we rotated between three predefined zig-zag transect routes (off-set by 2 km) in the coastal sites to increase sampling coverage (Fig. 2). Transect routes were designed using Distance 6·0 (Thomas *et al.* 2009).

In the robust design language, our primary periods corresponded to the four seasons in the Australasian calendar: winter (June to August); spring (September to November); summer (December to February) and autumn (March to May). For this study, we aimed to conduct at least five secondary occasions (i.e. consecutive surveys of the three sites) per primary period ($n = 16$); however, this was not successful for four primary periods because of weather conditions (Table S3). If a survey was interrupted because of weather conditions or logistical issues, the survey was cancelled and entirely re-run. Surveys of each site were conducted in random order and at different times of the day.

To limit violation of the closure assumption of a robust design (Pollock 1982; Nichols & Kendall 1995), we aimed to complete a secondary occasion in the shortest possible time (i.e. on consecutive days,

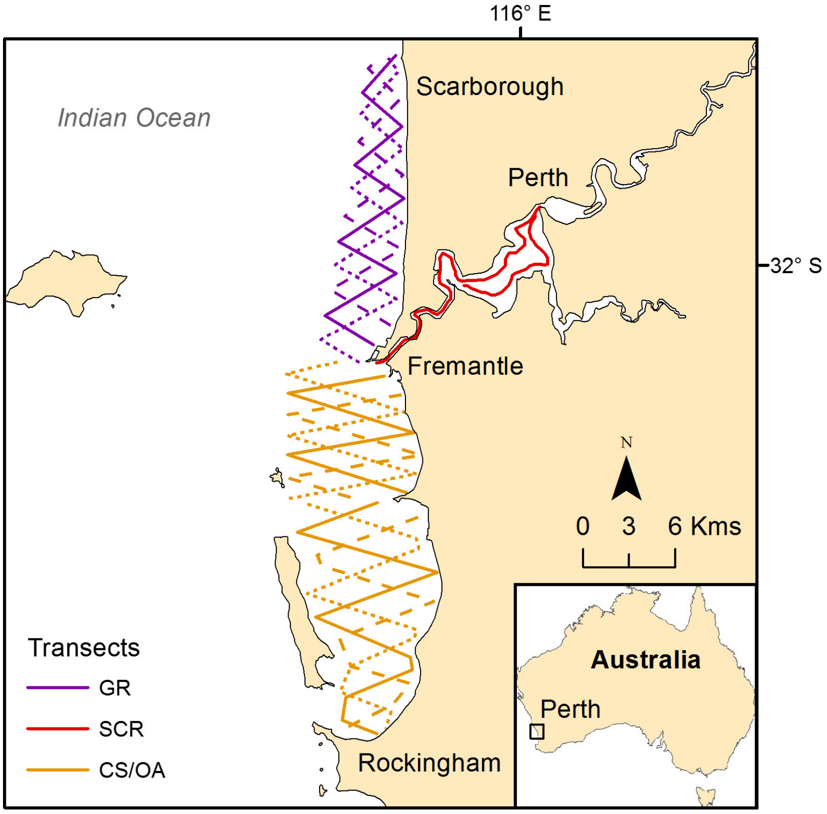

Fig. 2. Map of the metropolitan waters of Perth, Western Australia, showing the systematic survey routes within each site: the estuary SCR – Swan Canning Riverpark and the coastal sites (south to north) CS/OA – Cockburn Sound/Owen Anchorage, and GR – Gage Roads. Within the coastal sites, surveys were conducted by rotating between three predefined transect routes (full, long dash and short dash lines) to maximize the coverage.

mean = 2·60; min = 2; max = 8 days, Table S3) so as to minimize transitions of the animals (Pollock 1982). When multiple captures occurred for an individual in a secondary occasion, we retained only the first capture for that secondary occasion. We then waited for at least 1 week (unless weather conditions were excellent and/or we were approaching the end of the season – primary period) before starting another secondary occasion. The break between two secondary occasions was longer than the time needed to successfully complete a secondary occasion (mean = 8·63; min = 0, max = 60 days, Table S3), thus allowing us to assume independence between secondary occasions. We also left a longer interval between two adjoining primary periods (mean = 47·30; min = 12; max = 80 days, Table S3) to minimize violation of the assumption between closed and open sampling occasions (Kendall 2004; Brown *et al.* 2016). The assumption of closure within primary periods was tested with the program CloseTest (Stanley & Burnham 1999, see Appendix S1 for explanations in Supporting Information).

Data collection and data processing

To minimize heterogeneity of individual capture probabilities, the vessel was driven at a constant speed (8–12 knots) with at least three observers on-board to maximize the area coverage. However, 3% (10 of 304 surveys) of the surveys were conducted with two observers only. Surveys were conducted in Beaufort sea state ≤ 3. When a dolphin group was encountered along a transect route, we paused the search effort and photographed the dorsal fin of each individual on both sides (if possible) and without regard to the distinctiveness of fins. Photographic effort was conducted by the same person (DBHC) throughout the entire study period. In this study, dolphins were assigned to the same group when seen within approximately 100 m from the boat (Wells *et al.* 1987; Quintana-Rizzo & Wells 2001) and performing similar activities. Once all dolphins were photographed, the search effort was resumed from where we had departed the transect route. Photographs of each dolphin group were then graded for quality by one to three trained assistants and checked by DBHC for the entire study period. Measures of the quality and individual distinctiveness were done using modified methods developed by Urian, Hohn & Hansen (1999, see Appendix S3). Each individual was assigned a grade for distinctiveness of their dorsal fins to minimize misidentification and heterogeneity in capture probabilities (Nicholson *et al.* 2012).

To minimize heterogeneity in captures due to misidentification of non-distinctive fins (D3), only individuals with distinctive fins (D1 and D2, Appendix S3) were used in the MSCRD models. Abundance estimates were then adjusted to take into account the proportion of individuals in the population that were unmarked (D3) following the method described in Nicholson *et al.* (2012) (see Appendix S4 for calculation of the proportion of distinctly marked individuals). We also attempted to address individual heterogeneity in capture probabilities by including sex as an individual covariate (i.e. female, male or unknown). However, given that 50% of the individuals were not sexed ($n = 169$), we acknowledge that estimates obtained through MSCRD models may be overestimated for sexed individuals and underestimated for unsexed individuals (Nichols *et al.* 2004) and for that reason are not presented here (but see Appendix S5 for MSCRD analyses including sex as individual covariate). Calves, typically less than 4 years of age (Mann & Smuts 1998), were excluded from the analysis because of their dependence on their mothers (i.e. captures must be independent, Pollock *et al.* 1990). Heterogeneity in capture probabilities was tested by implementing goodness-of-fit tests for multistate models using the program U-CARE (Pradel, Gimenez & Lebreton 2005; Choquet *et al.* 2009).

STATISTICAL METHODS

The multistate closed robust design models were run in MARK (White & Burnham 1999) and estimated four parameters per site: (i) abundance (N), which is the number of individuals using the study area; (ii) apparent survival rate (φ), which is the probability of surviving and staying in a sample site; (iii) transition probability (ψ), which represents the probability of moving from one site to another; and, (iv) capture probability (P). Although transitions from and to the study area may have occurred (i.e. TE to an unobservable site), models with an unobservable site never reached convergence, and thus are not presented. The modelling approach assumes that no site transitions occurred within a primary period (Arnason 1972, 1973). However, we acknowledge that 2·6% of the captures violated this assumption. Two adjustments were made to minimize this violation. First, if an individual was captured in two different sites within a primary period, we retained captures matching the site of the first capture recorded in that primary period. Results were similar if the last capture was retained instead and therefore are not presented here. Second, we ran the MSCRD models for two different scenarios, including one that involved pooling sites so that transitions between sites were minimized. Scenario 1 represented the three sites as originally described in our study area and Scenario 2 had all of the coastal sites (CS/OA and GR) pooled together into a single Coastal site for comparison with the estuary (SCR).

In MARK, each MSCRD model combination was run with the probability of capture (P) varying by site and/or primary period or constant, and with recapture probability (c) set as equal to first capture probability (P). The abundance (N) was set to vary by site and primary periods [N(site × primary periods)]. Several sub-models for apparent survival (φ) were run (i.e. whether it varied by site and/or primary period or constant). Transition probability between sites (ψ) was also estimated, whether that parameter varied by site and/or primary period or if it did not vary. In MARK, time intervals between primary periods were specified as a fraction of a year (i.e. 0·25) to estimate annual apparent survival and annual transition rates when modelled as time constant.

Models were ranked using the Akaike information criterion (AIC_c, Burnham & Anderson 2002). The model with most support by AIC_c (highest AIC_c weight) was selected as the most parsimonious model. Models with $\Delta\mathrm{AIC}_c < 2$ were also considered to have support from the data (Burnham & Anderson 2002).

Results

EFFORT

Seventy-six secondary occasions (167 days of boat-based surveys) were completed between June 2011 and May 2015 (see Table S3). In total, 410 dolphin groups were encountered, ranging in size from 1 to 32 dolphins (mean = 5·7, SE 0·3; excluding calves, see Tables S4 and S5). We individually identified 346 dolphins, of which seven were well marked but were identified from poor-quality photographs, and were therefore excluded from further analyses. Among the 339 individuals, 134 individuals were excluded from the mark–recapture analyses because of insufficiently marked dorsal fins (see Table S6). The overall proportion of distinctly marked individuals was

0·78 (SE 0·02) and varied from 0·69 (SE 0·06) for individuals captured in GR to 0·80 (SE 0·02) for individuals captured in SCR.

MODEL SELECTION

Results from the program CloseTest indicated that the population was closed over 13 of the 16 primary periods, indicating that the assumption of population closure was satisfied on >81% of cases, with no significant gains or losses (Table S1). Goodness-of-fit (GOF) test results, based on multistate and subcomponent tests in U-CARE, suggested an overall heterogeneity in capture probability ($\chi^2 = 216{\cdot}551$, d.f. = 145, $P < 0{\cdot}01$, see Table S2 for summary of GOF tests). The estimate of the variation inflation factor $\hat{c}$ was <1 ($\hat{c} = 0{\cdot}75$), suggesting no substantial overdispersion, which meant there was no need for Quasi-likelihood (QAIC$_c$) adjustments to define the most parsimonious model (Cooch & White 2005). For Scenario 1 (three sites), the best-fitting model, based on the AIC$_c$ weight, was that capture probability varied by site and primary period [*P*(site × primary period)], apparent survival rate varied by primary period but not site [φ(primary period)] and transitions varied between sites [ψ(site)] (see Table S7). For Scenario 2 (two sites), the best-fitting model was that capture probability varied by site and primary period [*P*(site × primary period)], apparent survival varied by site [φ(site)] and transitions varied between sites [ψ(site)] (see Table S7). Due to having small numbers of animals, we did not allow for capture probabilities to vary among secondary occasions. Individual heterogeneity in capture probability was therefore not modelled (which can be accommodated in conventional RD analyses, given sufficient data) despite this frequently being found in photo-identification studies of cetacean populations.

Capture probabilities

Capture probabilities varied by site and primary period (Fig. 3). Regardless of the scenario, the SCR had high capture probability (mean, $\hat{P} = 0{\cdot}30$, min = 0·11, max = 0·52, SE 0·03). In contrast, capture probability in GR was low (mean, $\hat{P} = 0{\cdot}06$, min = 0·00, max = 0·12, SE 0·01; Fig. 3). Sighting frequencies showed that individuals with higher sighting frequency were seen in SCR (>17 sightings), whereas 50% of individuals observed in GR were seen only once (see Fig. S1). Probability of captures for CS/OA was moderate (mean, $\hat{P} = 0{\cdot}15$, min = 0·08, max = 0·27, SE 0·01; Fig. 3). Coefficient of variation (CV) of the estimated capture probability varied by site (Fig. S2) with GR having the highest CV ($CV_{\text{median}} = 30\%$), thus suggesting high heterogeneity in capture probability in comparison to CS/OA for which the CV was lower ($CV_{\text{median}} = 15\%$).

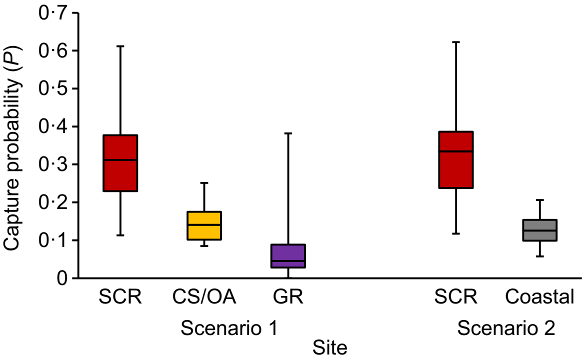

Fig. 3. Capture probability (*P*) yielded by the models for each secondary occasion represented as box plot (min; Quartile 1; median; Quartile 3; max) for each Scenario 1 – three sites (SCR, CS/OA and GR; and 2 – two sites (SCR and Coastal).

Apparent survival estimates and abundances

Models yielded apparent survival rates (φ) ranging from 0·93 (SE 0·03) to 1 (SE 0·00), although φ was higher in SCR ($\hat{\varphi}_{\text{SCR}} = 0{\cdot}98$, SE 0·04) than in the pooled Coastal site ($\hat{\varphi}_{\text{Coastal}} = 0{\cdot}83$, SE 0·02) in Scenario 2.

Total estimated abundances in the SCR were low but stable over the study period ($\hat{N}_{\text{total,SCR}} = 16$, min 10, max 23) (Fig. 4). Also, individuals were frequently resighted in the SCR (see Figs S1 and S3).

No obvious seasonal variation in abundance estimates was detected in the CS/OA site ($\hat{N}_{\text{total,South}} = 103$, min = 71, max = 147, Fig. 4). Abundance estimates in GR varied with the highest in winter 2011 ($\hat{N}_{\text{GR,max2}} = 172$, 95% CI 53–561) and autumn 2015 ($\hat{N}_{\text{GR,max1}} = 172$, 95% CI 78–381; Fig. 4). No dolphins were 'captured' in GR in summer 2012 and winter 2014.

Transitions

The estimates of the transition probabilities ($\hat{\psi}$) yielded by the model in Scenario 1 suggested that there was very little or no transition between the SCR and GR sites ($\hat{\psi}_{\text{SCR-GR}} < 0{\cdot}010$) (Table 1). The model yielded a higher transition probability from the SCR to CS/OA ($\hat{\psi}_{\text{SCR}\rightarrow\text{CS/OA}} = 0{\cdot}151$, SE 0·028) than in the opposite direction ($\hat{\psi}_{\text{CS/OA}\rightarrow\text{SCR}} = 0{\cdot}028$, SE 0·005). Estimates from Scenario 2 also indicated similar transition probabilities with higher transition from the SCR to Coastal sites ($\hat{\psi}_{\text{SCR}\rightarrow\text{Coastal}} = 0{\cdot}158$, SE 0·029) and a low rate in the opposite direction ($\hat{\psi}_{\text{Coastal}\rightarrow\text{SCR}} = 0{\cdot}017$, SE = 0·003).

Discussion

Three broad results emerged from our use of a MSCRD with geographic sites as 'states' in a complex coastal environment with estuarine, embayment and open coastline components and with a species known to exhibit fine-scale population structure in such systems. First, the heterogeneity of capture probabilities between sites showed a clear spatial component, consistent with some degree of population structuring. Second, estimates of abundance and apparent survival rate allowed some inference about the status of each site-related grouping (or 'subpopulation', in the metapopulation model). Finally, estimates of transition

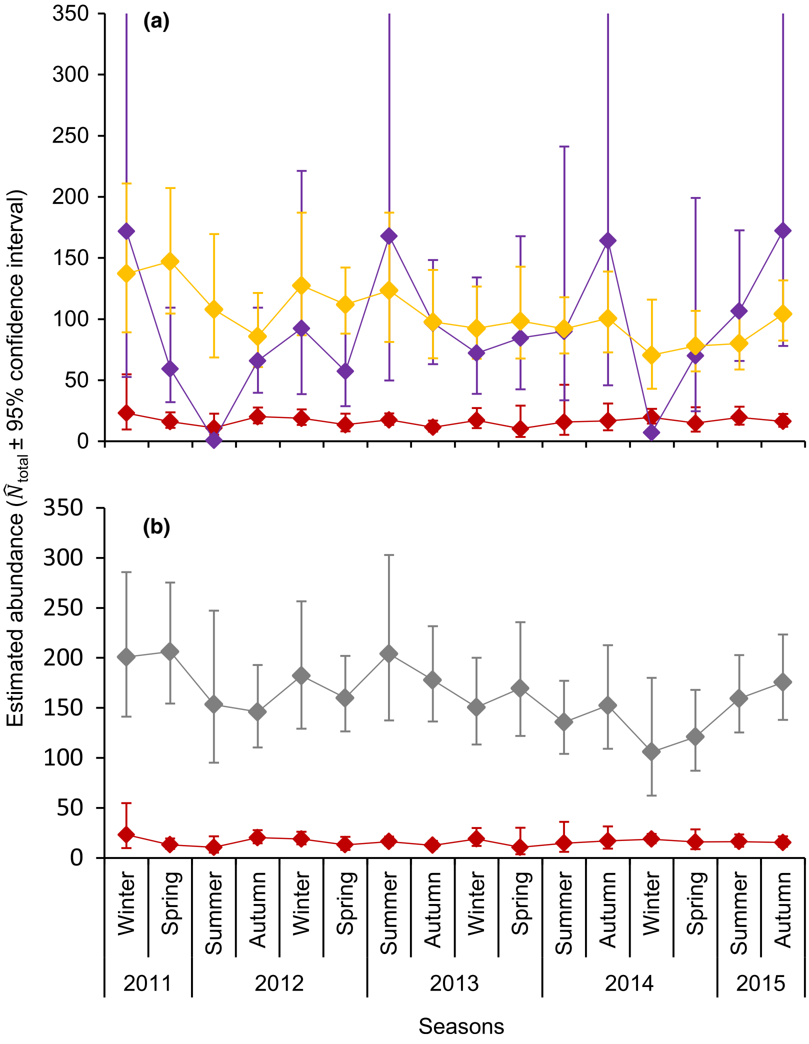

Fig. 4. Seasonal estimated abundances ($\hat{N}$ total ± 95% confidence intervals) for (a) Scenario 1 – three sites (SCR, CS/OA and GR) and (b) Scenario 2 – two sites (SCR and Coastal). Lines between data points have been used for illustrative purposes only; continuity of values is not implied. Sites are as follows: SCR (red), CS/OA (yellow), GR (purple) and Coastal in Scenario 2 (grey).

Table 1. Estimates of transition probability ψ (SE) between sites for (a) Scenario 1 (three sites: SCR, CS/OA and GR) and (b) Scenario 2 (two sites: SCR vs. Coastal)

Transition From:	Into: SCR	CS/OA	GR	Coastal
Scenario 1				
SCR	*0·840*	0·151 (0·028)	0·009 (0·008)	–
CS/OA	0·028 (0·005)	*0·921*	0·051 (0·009)	–
GR	0·000 (0·002)*	0·084 (0·014)	*0·916*	–
Scenario 2				
SCR	*0·842*	–	–	0·158 (0·029)
Coastal	0·017 (0·003)	–	–	*0·983*

Values in italic represent rates when staying in the same site.
*Values estimated were smaller than 0·001.

probability between sites indicated some degree of connectivity between those site-related groupings.

SPATIAL HETEROGENEITY

Differences in capture probability appear to reflect individual variation in the use of (and fidelity to) a site. Heterogeneity in capture probability has also previously been linked to variation in individual or group ranging patterns (Crespin *et al.* 2008; Urian *et al.* 2014). Here, the capture probability was high in the estuary (SCR) and low in the open coastline (GR), suggesting that the ranging patterns of dolphins using those sites differ markedly in, e.g. home range size, site fidelity, seasonal or year-round occupancy and habitat use (Sprogis *et al.* 2015).

The capture probabilities for the estuary are consistent with the long-term site fidelity and year-round occupancy reported in Chabanne *et al.* (2012). In contrast, Waples (1997) suggested that dolphins in the open coastline north of Perth likely range over many kilometres of coastline and are only intermittently present in particular areas, again consistent with the low capture probabilities observed here.

In addition, coefficients of variation for GR were high, suggesting more individual heterogeneity in capture probability due to factors such as large and variable home range sizes or avoidance or attraction responses to boats (Pollock *et al.* 1990). We acknowledge that the estimates of demographic parameters for GR could be biased with lower estimates of apparent survival leading to underestimated abundances (Pollock *et al.* 1990; Williams, Nichols & Conroy 2002). This outcome indicates the practical difficulties for MSCRD approaches if the ranging patterns (or other characteristics) of the individuals present at a site are such that CVs will be high, even where sampling is relatively intensive and is sustained over multiple years.

In contrast, the low coefficient of variation in the capture probabilities for CS/OA (CV = 15%) suggested that majority of the individuals were equally captured. Furthermore, despite lower capture probabilities than those estimated in SCR, dolphins nonetheless occurred year-round in CS/OA. Differences in capture probabilities between CS/OA and SCR may reflect larger home ranges for individuals in the embayment system (Sprogis *et al.* 2016). Site configuration may also influence individual detection with a greater likelihood of detecting individuals in narrow areas such as channels or rivers than in wide, unconfined areas such as open water that have no prominent barriers.

APPARENT SURVIVAL AND ABUNDANCE ESTIMATES

Given that the majority of the individuals were not sexed, we acknowledge that estimates of the apparent survival rates obtained through the best-fitting models may be overestimated for sexed individuals and underestimated for unsexed individuals. Also, most of the sexed individuals were those regularly seen during the study period because collection of genetic samples (for which sex determination was one objective) was preferentially undertaken on well-known individuals. While Nichols *et al.* (2004) demonstrated how to deal with unsexed individuals in capture–recapture analytical approaches, that method could not be applied in our study due to the complexity of the models. Apparent survival of dolphins in SCR was high (0·98), illustrating an almost complete lack of permanent emigration during the study. In addition, consistent abundance estimates across the course of the study (c. 16 dolphins), along with high individual resighting rates, indicated the long-term residency of the SCR subpopulation.

In contrast, an apparent survival estimate of 0·83 in the pooled Coastal site is indicative of permanent emigration of individuals, suggesting both resident and more transient components (Brown *et al.* 2014; Palmer *et al.* 2015). Variation in abundance estimates in conjunction with apparent survival rates can assist in making inferences about residency status (Brown *et al.* 2016). The high variability in abundance estimates in GR coupled with the large number of individuals sighted only once (and not seen in SCR or CS/OA) is consistent with transient occupancy patterns for dolphins at that site. This agrees with other studies indicating that bottlenose dolphins are often more abundant in open coast environments where individuals tend to have larger home range size, which may reflect both food availability and foraging tactics (Sprogis *et al.* 2015; McCluskey, Bejder & Loneragan 2016).

TRANSITIONS

There was a substantial difference in transition probabilities between the SCR and the coastal sites. The reasons for this are not clear. As the mouth of the SCR estuary is located at the junction between the CS/OA and GR sites, travel distance between sites should not be a factor. Furthermore, transitions from SCR were also limited to CS/OA. One possibility is that the environment of OA (shallow, protected waters with extensive seagrass meadows) may be more suitable habitat for SCR individuals than the GR environment.

Conversely, transitions from CS/OA to SCR were limited, although occasional visitors were documented in the lower reaches of the estuary or further up river, sometimes escorted by SCR males (Connor *et al.* 1996; Connor, Read & Wrangham 2000). Those transitions in and out from SCR were consistent with the emigration and reimmigration demographic model reported in Chabanne *et al.* (2012). The long-term connection between SCR and CS/OA suggests a certain degree of gene flow between the subpopulations.

LIMITATIONS

The transitions of animals in and out of the study area (i.e. sometimes referred to as the ‘edge effect’, Otis *et al.* 1978) present two significant problems for MSCRD studies. The first is that these transitions increase the heterogeneity of captures in the study area at large (Crespin *et al.* 2008; Brown *et al.* 2016). The second is that sites within the study area may differ in the degree to which such edge effects occur. In this study, for example, we found more heterogeneity associated with edge effects in the open coastline (GR) than in the estuary (SCR). When considering predefined sites, it is advisable to consider what proportion of the individuals captured in that site may also be captured in other sites and whether individual heterogeneity in capture probability may differ between sites. This is particularly relevant if sites differ greatly in size or in other features that may limit detectability and the precision of estimation (Burgess *et al.* 2014; Palmer *et al.* 2015). Here, we benefitted from existing information on the likely ranging patterns of individuals, but were nonetheless unable to implement a study design that negated the heterogeneity of captures arising from the transitions of individuals into and out of the study area.

The assumption that no transition between sites occurs within a primary period (Arnason 1972, 1973) is difficult to validate, particularly when sites are juxtaposed (i.e. no physical barrier and distance exists). Such violations may result in greater heterogeneity in capture probability between individuals and within sites (i.e. individuals captured within a site do not all have the same survival rate). Here, 2·6% of the captures violated this assumption. The extent to which this assumption can be acceptably violated remains unclear, although it has been reported that <1% of violated occasions would create a small bias (O'Connell-Goode, Lowe & Clark 2014). This issue was dealt with in our study by pooling the coastal sites (Scenario 2) (Schwarz 2002), while also ensuring that all states were sampled equally (Crespin *et al.* 2008). However, this procedure may lead to more heterogeneity in capture probabilities and bias survival rates and abundance estimates (Pollock *et al.* 1990). Here, the survival rate for dolphins in CS/OA was higher than for GR, which was also supported by a consistency in abundance estimates and moderate resighting rates in CS/OA with few individuals being seen only once.

Low capture probabilities make it difficult to obtain reliable estimates of apparent survival rate and abundance (Pollock *et al.* 1990; Rosenberg, Overton & Anthony 1995). It is advisable that capture probabilities of at least 0·10 per secondary occasions be obtained for reasonable results (Lettink & Armstrong 2003). Although common in studies of wide-ranging and low-density species (Harmsen, Foster & Doncaster 2010; Palmer *et al.* 2015), there are few obvious measures for dealing with low capture probabilities other than increasing sampling effort (Pollock *et al.* 1990; Rosenberg, Overton & Anthony 1995). However, increases in sampling effort involve additional cost (Tyne *et al.* 2016) and time outlays that must be multiplied by the number of sites (to ensure that each site is surveyed equally).

Finally, we note that the sophistication and utility of MSCRD models continue to evolve, notably in relation to the modelling of TE, which can alleviate some of the large differences in survival estimates (Bailey, Converse & Kendall 2010). We were unable to model TE in this study as our models would not estimate the applicable parameters, due to the small population sizes. Rankin *et al.* (2016) also discussed issues linked to low capture probabilities and the estimation of TE and suggested use of hierarchical Bayesian models for the Robust design.

Conclusion

This study, which explored the implications of heterogeneity in capture probabilities for MR studies within a MSCRD framework, demonstrated a valuable approach for assessing the dynamic, status and connectivity of multiple subpopulations of a behaviourally plastic species within a heterogeneous environment. We also showed that a MSCRD study design can assess transitions between predefined geographic sites, and thus assist in understanding dynamic processes between subpopulations within a metapopulation. A MSCRD incorporating geographic sites associated with anthropogenic impacts or climate change may be a powerful tool for management and conservation of species that are amenable to a MR study. The short-term transition of individuals between putative subpopulations is particularly relevant for the conservation of highly mobile species (e.g. birds, larger mammals) in environments where anthropogenic pressures vary greatly from one geographic 'site' to another.

Authors' contributions

D.B.H.C., H.F. and L.B. conceived the study; D.B.H.C., K.H.P. and L.B. designed methodology; D.B.H.C. collected data; D.B.H.C. and K.H.P. analysed the data; D.B.H.C., H.F. and L.B. wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data accessibility

The dataset used in this manuscript will be made available in the Dryad data repository DOI: https://doi.org/10.5061/dryad.24s3c Data files: Mark_files (Chabanne *et al.* 2017).

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Supporting Information

Details of electronic Supporting Information are provided below.

Appendix S1. Description of the CloseTest: a method to investigate the population closure.

Appendix S2. Test for heterogeneity in capture probabilities by implementing goodness-of-fit tests for multistate models using the program U-CARE.

Appendix S3. Data processing for photograph quality and individual distinctiveness.

Appendix S4. Method to estimate proportion of distinctly marked individuals and correction of the marked abundance estimates for consideration of the proportion of unmarked individuals (D3 individuals identified from Q1 and Q2).

Appendix S5. MSCRD analysis using sex as an individual covariate.

Table S1. Closure tests for each primary period using Stanley & Burnham (1999) and Otis *et al.* (1978) implemented in the program CloseTest.

Table S2. Summary of U-CARE test results for bottlenose dolphin study during 2011–2015.

Table S3. Summary of survey effort and time interval between efforts across primary periods (i.e. seasons) for 4 years (June 2011–May 2015).

Table S4. Number of dolphin groups per site and per season of each year (16 seasons, 4 years, aka primary periods).

Table S5. Group size (Mean, SE, Min and Max) per site and per season of each year (16 seasons, 4 years, aka primary periods).

Table S6. Summary of the number of identified individuals of bottlenose dolphins (*and marked only*) by site in each season of each year (16 seasons, 4 years) and from good photo quality only.

Table S7. Summary of the top three multistate closed robust design models (in rank order of AIC_c scores) for each scenario: Scenario 1 with three sites and Scenario 2 with two sites.

Fig. S1. Sighting frequency of adult/sub-adult dolphins observed in the metropolitan waters of Perth from June 2011 to May 2015.

Fig. S2. Coefficient of variations (CV) of each capture probability (P) for each Scenario.