Meta- and subpopulation estimation with disparate data: coconut crabs in the Western Indian Ocean

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Abstract

Widely dispersed fragmented populations are a challenge to monitor because subpopulation sizes may be very small, difficult to access and time consuming to sample regularly. We use the coconut crab (*Birgus latro*) on Pemba, United Republic of Zanzibar as a case study for estimating highly fragmented populations and metapopulation sizes. The species is a very large terrestrial decapod threatened by exploitation and habitat alteration and now classified as vulnerable. We developed an integrated model to analyse capture-mark-recapture (CMR) data from five sites jointly with count data from 24 sites to estimate site-level densities and population sizes, predicted total population size across the Pemba archipelago, and investigated the effect of six predictors of human influence on density. We fitted separate models to test the effect of the same predictors on raw counts and individual body mass. We estimate the total population of coconut crabs on the Pemba archipelago to be *c*. 6700 terrestrial individuals. We show that government protection generally affects crabs positively, whereas presence of agriculture negatively affects their densities. This study highlights that time-consuming CMR data can be leveraged to estimate densities on less visited sites, and that fully protected islands are critical for maintaining relatively high population densities. Our overall population estimate suggests that Pemba still hosts a viable coconut crab population in a part of its range where the species is otherwise in steep decline.

Introduction

As populations become ever more fragmented, they are increasingly challenging to monitor because isolated subpopulations can be difficult to reach and their dwindling sizes can result in sparse data being collected. Nonetheless, the sizes of small subpopulations are important especially if they are connected through immigration and are capable of recolonizing each other (metapopulations, Hanski & Simberloff, 1997). Sometimes fragmented populations enjoy partial protection in one part of their range but not elsewhere and these protected subpopulations can potentially act as sources in a metapopulation (Hansen, 2011). This makes it particularly important to know the subpopulation sizes of those fragments under protection.

One major challenge in estimating population size is that of imperfect detection—we cannot know whether we have counted all individuals in the sampled population, and in most cases, we likely have not. Capture-mark-recapture (CMR) models (Otis *et al*., 1978) are the gold standard of abundance estimation but require repeated visits to sampling sites, which is challenging if the number of subpopulations to monitor is numerous and their locations are remote or widely dispersed. These models also require sufficient individuals to be captured and recaptured, which is especially difficult to achieve at depauperate sites.

Jointly analysing data from all subpopulations in a hierarchical CMR model (Converse & Royle, 2012) can address the challenges of sparse data for some subpopulations. These models allow sharing information on detection probability among subpopulations, thus enabling detection-corrected estimates of abundance even for subpopulations where data are sparse. In the context of metapopulation estimation, however, subpopulation level observations may range from CMR data

to single counts, due to logistical constraints and/or small size of some subpopulations. Integrated models can combine such disparate data within a single statistical model (e.g. Schaub & Abadi, 2011; Zipkin *et al.*, 2021). The framework leverages high-resolution information often only available at small scales (e.g. CMR data, systematic species occurrence surveys) and combines it with lower resolution data (e.g. counts, opportunistic occurrence data) that can be collected at larger scales, to assess population status and dynamics at large spatio-temporal scales (e.g. Chandler & Clark, 2014; Pacifici *et al.*, 2017). This makes integrated modelling a suitable framework for metapopulation estimation and monitoring.

Here, we present a test case of subpopulation estimation using a rare arthropod species to exemplify how integrating CMR and count data can address the challenges of data disparity among subpopulations. We further provide a baseline estimate of the coconut crab (*Birgus latro*) population on Pemba, Zanzibar, one of its last strongholds in the Western Indian Ocean, against which future monitoring efforts can be compared.

Coconut crabs are the world's largest terrestrial arthropod reaching 4 kg in body mass and 1 m in leg span (Brown & Fielder, 1991; Drew *et al.*, 2010). Following a short larval stage at sea, individuals move on to land, where very young stages carry an empty mollusc shell, and generally remain in coastal scrub or forest for the rest of their lives, never entering water again (Brown & Fielder, 1991). Coconut crabs are almost immune to natural predation but are threatened by anthropogenic exploitation for food and habitat destruction owing to agricultural expansion and coastal housing and hotel development (Cumberlidge *et al.*, 2022). Now, virtually extirpated from continental landmasses, coconut crabs are mostly found on island archipelagos across the Indian Ocean and Western Pacific Ocean. As a result of these threats, this species has recently been upgraded from 'Data Deficient' to 'Vulnerable' on the IUCN Red List (Cumberlidge, 2020).

Coconut crab populations on most island archipelagos in the Western Indian Ocean are in steep decline or else extirpated (Cumberlidge *et al.*, 2022). Despite this, the species still survives on some coastal East African islands and on Unguja and Pemba, Zanzibar, although principally on outlying smaller islands off the Zanzibari coastline (Caro *et al.*, 2021; Hamad *et al.*, 2023). Here, our aim was to: Estimate the abundance and density of coconut crabs on the main island of Pemba and its outlying islands (Fig. 1), investigate the effect of six predictors of human influence on density and derive a total population size for the Pemba archipelago. To do so, we build an integrated model combining data from CMR surveys of five coconut crab subpopulations with count surveys from 24 additional subpopulations within or near the Pemba archipelago. We focus here on estimating population sizes, but the flexible modelling approach can form the basis of regional metapopulation monitoring, for harvesting or setting quotas, and can be adapted to other metapopulation estimation situations.

Materials and methods

Study sites

The research was principally conducted on the island of Pemba and its outlying islands in the United Republic of Zanzibar archipelago, across 29 sites. Pemba (988 km^2, 26 of the sampled sites) is an oceanic island lying 50 km east of the Tanzania mainland. The island is hilly with fertile soil. Pemba is dominated by small-scale farming of cassava, tomatoes, bananas, with cloves (*Syzygium aromaticum*) as the cash crop. It has a large human population of 400 000 people. Unguja (1666 km^2, one sampled site), the other main island in the Zanzibar archipelago, is a Landbridge island lying 59 km to the south. The island is flat and relies heavily on the tourism industry as well as fishing and considerable seaweed farming; 900 000 people live there. Two uninhabited islands in the Dar es Salaam Marine Reserve system were also sampled for crabs (Fig. 1); these islands comprise sandy and rocky karst beaches with mostly sandy interiors.

Field data collection

TC conducted searches of adult coconut crabs (defined as individuals that had lost their gastropod shell and were fully terrestrial) on all sites (Fig. 1), several repeatedly, between July 2016 and August 2022; JZ surveyed Misali Island in April 2022; and L-MG visited Chumbe in June–July 2022 (for details on surveys, see Appendix S1, Tables S1 and S2). Survey periods were principally in the early part of the dry season to maximize the number of nights that could be spent searching in the field, except for Misali which was surveyed in the wet season. Sampling sites were identified based on local information, and areas to search within those sites were chosen by local fishermen or farmers familiar with the area and who usually took part in the surveys. Groups of between one and six persons (mean = 2.57 ± 1.26 persons; $N = 154$ nights) conducted crab surveys along transects or within search areas. Surveyors, spread out and equipped with torches, walked slowly starting between 19.15 and 20.30 h and continued for 2–4.5 h. We recorded total search effort daily as total time spent in the field.

Once detected, each crab was captured and placed in a bucket, weighed, sexed and measured. Before release, it was photographed and marked with a uniquely assigned number using a white marker (Edding 950 industrial painter) lasting the length of a survey (maximum 3 months), so that subsequent recaptures could be identified (see also Oka *et al.*, 2013).

Surveys consisted of one or multiple visits (defined as one night searching, also referred to as sampling occasions) to the same site within a season (between December and April, or between June and September). There were four types of surveys: (i) on Pemba mainland sites conducted by TC (Fig. 1), usually repeated sampling occasions separated by a minimum of a week, with total survey length not exceeding 3 months; (ii)
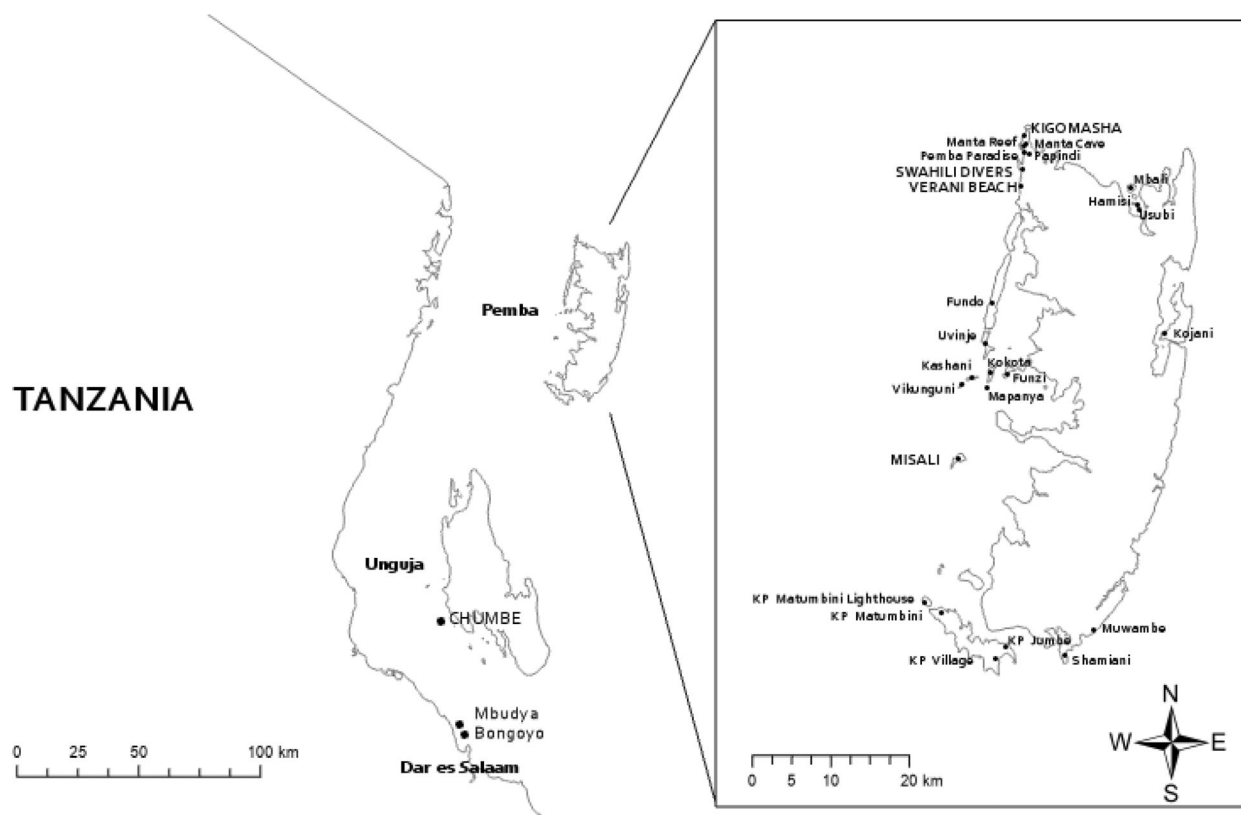
Figure 1 Sites where coconut crabs (*Birgus latro*) were sampled on Zanzibar, Tanzania, showing Pemba to the north and Unguja to the south. Also shown are Bongoyo and Mbudya islands near to Dar es Salaam. Insert shows Pemban sites; locations in capitals refer to sites from which capture-mark-recapture data were obtained.

on islands off the coast of Pemba (where additional sampling occasions would be prohibitively difficult) by TC and RSR, either one night, or two consecutive nights; (iii) on Chumbe island by TC up to five consecutive nights, with one survey consisting of two such bouts within 2 months; and (iv) on Misali and Chumbe islands by JZ and L-MG, repeat sampling occasions, approximately twice or once per week, respectively, and over a span of 3–11 weeks respectively.

Modelling framework

We approached our objective in two steps, implemented in a Bayesian framework: (1) Fitting an integrated model that combines closed population CMR modelling (Otis *et al*., 1978) for a subset of surveys with appropriate data, and N-mixture modelling (Royle, 2004a) for the remaining surveys, to estimate density and its drivers across sampled sites; (2) using posterior prediction from the integrated model to extrapolate abundance to suitable habitat throughout the sampled sites.

Population closure

CMR models assume that populations are closed (i.e. do not change) over the course of a survey. We are confident

that within the maximum 3-month survey duration recruitment into the sampled 'adult' population (having discarded their mollusc shell) was negligible since very small individuals were rarely caught. Crabs are nocturnal so suffer little avian predation and there are virtually no mammalian predators on small islands in our study area (Foley *et al*., 2014) with the possible exception of rats (*Rattus rattus*) on some islands (e.g. Mapanya and Misali) that may take small coconut crabs (<0.15 kg) lacking mollusc shells. The main source of mortality of coconut crabs is harvest by humans but offtake is infrequent and irregular on most islands even where they are persecuted by children, with only two dead crabs encountered during 7 years of study. Closure can also be violated by movement off the search area. Several sampled sites were on very small islands (<20 ha) or surrounded by unsuitable habitat (see definition below) with little room for crab movement (<15 ha) such as Verani (see Table 1); however, there may have been movement off the search area on larger islands (e.g. KP Matumbini, Misali, Fundo and Ngao). This is a common problem in studies applying CMR or N-mixture models; however, as long as movement in and out of the search area is random, this lack of closure does not bias estimates of the number of animals that use the search area (Kendall, 1999).

Table 1 Summary of survey effort for coconut crabs (*Birgus latro*), catch per unit effort (CPUE = individuals caught per 100 min sampled, averaged over all surveys at a site), and estimates of density (D; crabs/ha) and abundance across all suitable habitat at a site (posterior mode and upper/lower 90% Bayesian credible interval limits, 90% BCI) from integrated model of capture-mark-recapture (CMR) and count data, for 29 sites in/near the Pemba Archipelago, Tanzania. Sampled area = area physically searched for crabs plus 100-m buffer minus unsuitable habitat (ha); site area = total area of suitable habitat at a site (ha); Surveys (nights) = total number of surveys (total nightly visits)

Site	Sampled area	Site area	Surveys (nights)	CPUE	Density (90% BCI)	Abundance (90% BCI)
Protected islands						
Chumbe[a,b]	3.78	15.8	5 (36)	11.49	41.97[c] (31.93–55.92)	214.83 (163.41–286.21)
Misali[a]	13.18–23.13[d]	83.8	7 (23)	6.75	2.56 (1.59–5.75)	214.21 (133.51–482.07)
Bongoyo[b]	30.15	70.5	1 (2)	3.32	2.35 (1.43–6.47)	165.97 (100.50–456.43)
Mbudya[b]	27.25	55.4	1 (2)	4.81	3.74 (2.22–9.28)	206.99 (123.08–514.23)
Vicinity of hotels						
Swahili Divers[a]	29.6	29.6	8 (27)	3.29	3.12 (2.03–5.46)	92.32 (60.05–161.72)
Verani[a]	13.3	13.3	6 (17)	1.81	1.98 (1.31–4.09)	26.3 (17.40–54.37)
Pemba Paradise	1.3	1.3	2 (2)	1.91	13.6 (6.51–49.62)	17.67 (8.47–64.51)
Manta lighthouse	19	19	1 (1)	2.94	2.84 (1.37–8.92)	53.96 (26.12–169.45)
Shamiani	50.37	383	2 (4)	1.01	0.45 (0.24–1.26)	172.91 (92.86–484.15)
Pemba mainland						
Kigomasha[a]	25.9	25.9	8 (21)	2.92	4.97 (3.09–11.77)	128.72 (80.08–304.78)
Papindi	8	8	2 (3)	1.82	4.71 (2.45–11.98)	37.7 (19.57–95.80)
Manta Cave	1	1	2 (3)	1.11	14.22 (5.82–47.66)	14.22 (5.82–47.66)
Muwambe	124.55	124.55	1 (1)	0	0.07 (0.02–0.66)	8.16 (2.98–82.70)
Inhabited islands						
Fundo	79.4	801	5 (10)	3.94	1.11 (0.79–1.90)	892.12 (636.72–1521.43)
Matumbini village KP	16.4	386	1 (1)	0.69	0.64 (0.23–4.25)	245.61 (90.51–1642.12)
Kojani	14.1	14.1	1 (1)	2.5	2.46 (1.04–9.40)	34.74 (14.62–132.59)
Ngao	47.61	476	2 (2)	1.23	0.5 (0.24–1.67)	236.57 (113.64–796.67)
Kokota	18.82	79.4	3 (3)	2.82	3.33 (2.08–6.78)	264.22 (165.23–538.10)
Uvinje	26.05	87.9	1 (1)	0	0.18 (0.06–2.19)	16.03 (5.29–192.84)
Funzi	35.37	88	1 (1)	0	0.17 (0.06–1.85)	14.53 (4.88–162.44)
Uninhabited islands						
Jombe KP	36.05	66.6	4 (4)	5.65	3.51 (2.34–6.17)	233.65 (156.02–410.74)
Matumbini KP	43.74	731	4 (5)	6.64	3.71 (2.66–6.51)	2713.59 (1948.04–4762.20)
Matumbini lighthouse	9.15	75.8	1 (1)	1.33	1.05 (0.41–8.18)	79.81 (31.40–620.41)
Kashani	11.89	28.2	1 (1)	1	0.83 (0.32–5.97)	23.54 (8.93–168.49)
Vikunguni	8.4	15.3	1 (1)	2.07	3.1 (1.44–13.52)	47.42 (22.11–206.87)
Mapanya	2.52	5	1 (1)	2.5	8.48 (3.65–40.57)	42.41 (18.27–202.83)
Usubi	14.8	14.8	1 (1)	0	0.29 (0.07–3.46)	4.26 (1.10–51.21)
Hamisi	2.78	2.7	1 (1)	0	0.52 (0.12–8.87)	1.4 (0.33–23.95)
Mbali	46.98	58.1	1 (1)	0	0.15 (0.05–1.65)	8.78 (2.84–95.86)
Pemba archipelago						6687.97 (5050.58–10443.55)

[a] Site with capture-mark-recapture surveys.

[b] Sites not part of the Pemba archipelago.

[c] Density only for lodge area (area of highest density on the island).

[d] Based on three transects and one search area.

Accounting for crab movement

For all analyses, we defined the sampled area as the area physically searched (henceforth, search area) plus a 100-m buffer, from which we removed unsuitable habitat, defined as cleared agricultural land, mangroves, seawater or houses. Buffering is necessary to account for individual movement on and off the search area (Otis *et al.*, 1978; Wilson & Anderson, 1985). Typically, these buffers are thought to represent an average home-range radius but information on coconut crab movement is sparse. Typical movement radii

range from <10 m (Fletcher, Brown, & Fielder, 1990; Helfman, 1973; Oka *et al.*, 2016) to 62 m (Krieger *et al.*, 2012), with long distance movements of several km (Krieger *et al.*, 2012). In one of our own surveys, the maximum recapture distance was 226 m, with an average of 46 m. To be conservative in the sense of not overestimating crab populations, we opted for a 100-m buffer. This is necessarily subjective and choosing a different buffer would alter estimates of densities and population sizes. By adopting one consistent buffer, we aim to make density estimates comparable across all surveyed locations. For some (particularly non-

island) sites, sampled areas covered all the suitable habitat and were thus equal to the total area of suitable habitat of that site. But many (generally island) sites had suitable habitat beyond the sampled area. For these sites, we defined the total area of suitable habitat as the total island area minus area covered by houses, agriculture or mangroves. Sampled areas and total area of suitable habitat were mapped out in Google Earth (14 December 2015 version) to determine their size in ha.

Integrated model

We developed a hierarchical integrated model that allowed us to estimate site-level abundance and density combining data from the different types of surveys described above. Broadly, we divided surveys into CMR and count surveys. Three issues prevented us from treating all surveys as CMR surveys: (1) before 2018, surveys did not reliably keep track of individual crab identity; (2) many surveys consisted of a single visit; (3) many surveys had no recaptures. We identified five sites with 22 post-2017 multiple-visit surveys and at least one recapture (Appendix S1, Table S1): Swahili Divers, Verani, Kigomasha (Pemba mainland), Chumbe and Misali (islands, Fig. 1). For these surveys, we developed a CMR observation model. For all other count surveys, we developed an N-mixture (Royle, 2004a) observation model. Whereas it is conceptually possible to develop an all-CMR model including single-visit surveys and surveys without recaptures, such a model would have to exclude 16 pre-2018 surveys (or 21% of all surveys), which is not desirable, especially in a sparse data situation like ours. Moreover, the loss of information in N-mixture models (due to ignoring individual identity) only occurs in count surveys with >1 visits; only 38% of count surveys had >1 visit. Finally, trials with an all-CMR model suggested it would be much slower to fit (i.e. multiple days with a 2.6 GHz processor with 64 GB RAM if chains can be run in parallel) than our combined model (several hours). An all-N-mixture model, on the other hand, would forego the information contained in the more detailed individual encounter data used in CMR models. Therefore, we opted for this hybrid approach.

The ecological model shared by all surveys describes expected abundance in survey j, λ_j, as

$$\log(\lambda_j) = \gamma 0 + \log(\text{area}_j) + \varepsilon_{s[j]} \tag{1}$$

Here, log is the natural logarithm, $\gamma 0$ is an overall intercept, $\log(\text{area}_j)$ is an offset to account for variation in size of the sampled area (ha) across surveys and ε_s is a site-level random effect (Normally distributed with mean 0 and SD = $\sigma.ran$) to account for surveys being nested within sites, s. Average site-level density (crabs/ha) can be derived as $D_s = \exp(\gamma 0 + \varepsilon_s)$. This 'Null model' can be expanded to include site-level covariates (see Drivers of density). Modelling of the latent realized survey-level abundance, N_j, depends on the observation model.

CMR observation model

For the 22 surveys identified as suitable for CMR analysis, we compiled individual encounter histories, marking whether or not an individual crab i had been detected ($y_{ijk} = 1$) or not ($y_{ijk} = 0$) on visit k nested within survey j. These observations are modelled as Bernoulli random variables with success probability = detection probability, p_{jk}. We estimated p_{jk} on the logit scale as a function of visit-level effort (duration of a field visit in minutes, divided by 100 to avoid numerical issues with very small coefficients). Because survey-level data were fairly sparse (Appendix S2, Table S1), we estimated detection parameters (intercept and effect of effort) for each site but kept them constant for all surveys within a site. Most searches were implemented by TC, except for three on Misali by JZ and one on Chumbe by L-MG. To account for potential different detection parameters due to different observer skill level and variation in sampling protocol, we estimated separate detection parameters for observers; for simplicity, that is omitted from the following equation.

$$\text{logit}(p_{jk}) = \alpha 0_{s[j]} + \alpha_{s[j]} \times \text{Effort}_{jk}$$

Here, $\alpha 0$ and α are site (and observer)-specific intercepts and effort effects. We arrived at the detection model structure using maximum likelihood analysis of only the CMR survey data and AIC-based model selection, described in Appendix S2.

We estimated abundance for each CMR survey using data augmentation (Royle, Dorazio, & Link, 2007). In data augmentation, the n_j observed encounter histories for each survey are augmented up to a large number, M_j, with all-0 encounter histories representing potential individuals. The model then estimates an inclusion parameter for each individual, z_{ij} as a Bernoulli random variable (1 if the individual is part of the population and 0 otherwise) with inclusion probability ψ_j, and abundance for a given survey N_j is derived as the sum of all $\mathbf{z}_j$. To link ψ_j to the expected abundance model (Equation 1), we calculated ψ_j as λ_j/M_j (note that this requires setting M_j large enough that ψ_j never exceeds 1). We found that this model was insufficient to account for variation in N_j among surveys. We therefore modelled ψ_j as a beta random variable with mean $\overline{\psi}_j = \lambda_j/M_j$ and standard deviation σ_ψ.

N-mixture observation model

For all surveys identified as not suitable for CMR analysis, we compiled the number of crabs detected at each visit, m_{jk}. The N-mixture model treats m_{jk} as a binomial random variable with number of trials = abundance N_j, and success probability = detection probability p_{jk}:

$$m_{jk} \sim \text{Binomial}(N_j, p_{jk})$$

$$\text{logit}(p_{jk}) = \beta 0_{p.\text{index}[j]} + \beta_{p.\text{index}[j]} \times \text{Effort}_{jk}$$

Here, p.index is a site-specific index for pre-2018 surveys from the five sites included in the CMR observation model (so that the site-specific detection parameters are used); for all other surveys, $\beta 0$ and β were defined as the average detection parameters ($\alpha 0$ and α) over all surveys implemented by TC (as all non-CMR surveys were implemented by TC). As these averages are calculated at each iteration of the MCMC algorithm, error in $\alpha 0$ and α is fully propagated to $\beta 0$ and β.

We modelled abundance N_j as a negative binomial random variable with mean λ_j from equation 1:

$$N_j \sim \text{NegBin}(\lambda_j, r)$$

Here, r is the overdispersion parameter of the negative binomial distribution. The negative binomial distribution can be thought of as a Poisson-Gamma mixture, where the Poisson mean is a random variable with a Gamma distribution. Thus, this realized abundance model mirrors the one for the CMR observation model, treating expected abundance as a random variable to better account for variation in N_j among surveys.

Drivers of density

In addition to the 'Null model' for expected abundance described in equation 1, we also fit models (with identical offset and random effect structure) testing the effect of six site-specific binary covariates on density. This analysis expands on a previous analysis of catch per unit effort (CPUE) data and body mass across a subset of 12 sites (Caro *et al.*, 2021). According to those results, we expected density to be lower at sites with presence of fishermen camping overnight and nearby permanent settlements (i.e. within walking distance: 3 km); and higher at sites with presence of agriculture (beans, maize, tomatoes or casava planted in adjacent agricultural land), unofficial protection within or near hotel grounds, being located on islands which are less influenced by humans, and having government protection. We only fit single-covariate models, because number of sites in some of these binary categories was low (Appendix S1, Table S2).

Posterior prediction of population size in suitable habitat

To obtain estimates of total abundance across all sampled sites, N.tot$_S$, for all sites except Chumbe, we multiplied site-level density D_s with the total area of suitable habitat at that site. For Chumbe, all searches were performed in the 'lodge area', the area of highest crab density on the island. To estimate population size for the remaining northern and southern parts of the island, we used reported proportions of crabs captured (73.8% in the lodge area, 8.9% in the north, 17.3% in the south) in an earlier study that sampled all three regions (Kilstromer & Bergwall, 2013). We calculated expected abundance in the lodge area, N_L, according to equation 1; expected abundance in the south and north,

$N_{\text{SN}} = N_L \frac{(8.9+17.3)}{73.8}$, and $N.\text{tot} = N_L + N_{\text{SN}}$. This approach depends on the assumption that (a) Kilstromer & Bergwall (2013) searched similar sized areas in all regions so that number of crabs captured was not affected by size of the sampled area and (b) that capture probability was similar in the three regions. Neither assumption can be tested; but the alternative of using lodge-area density for the entirety of Chumbe would severely overestimate total population size. Finally, to obtain total population size for the Pemba archipelago, N_{Pemba}, we summed N.tot over all sites that are part of the archipelago (Table 1). We performed all calculations on 5000 randomly selected posterior samples of the integrated model without covariates.

Note that our focus is on estimating population size, rather than change in population over time. We therefore base our abundance estimate on the site-level expected abundance, which is constant over time. This means that subpopulation estimates refer to different time scales (for single survey sites, they represent that point in time only, whereas for multiple survey sites, they represent an average over surveys). As there is no survey period in which all sites were visited, estimating abundances for a unified time frame is not possible with the present model and data.

Models of crab counts and body mass

Further expanding on the analysis by Caro *et al.*, 2021, we also tested the effect of the six potential drivers of density on raw crab counts and body mass (in kg). We analysed raw counts to ensure that results can be compared to potential future studies that may not want (or be able) to estimate abundance/density. We modelled survey-level counts (i.e. aggregated across visits) as negative binomial random variables with total survey-level effort as offset. This is akin to modelling counts per unit effort, where a unit effort is 100 min of field work. Body mass is a measure of body size (Sato *et al.*, 2013) which is a predictor of reproductive potential of coconut crabs (e.g. Sato & Suzuki, 2010) and thus an additional important indicator of subpopulation status. We modelled square root-transformed body mass as normal random variables; we allowed for site-specific residual variances to account for heteroscedasticity. We only included body mass measures from surveys carried out by TC to maintain consistency. We expected the same effects for counts and body mass as described for density. All models contained a site random effect; models for body mass also contained an effect of sex since the species is sexually dimorphic.

Model implementation

We implemented all models in Nimble (de Valpine *et al.*, 2017) using the R package nimble ver. 0.12.2 (de Valpine *et al.*, 2022) in R ver. 4.2.1 (R Core Team, 2022). We ran three parallel chains, each with 100 000 (integrated models) or 75 000 (count, body mass models) iterations, of which we discarded 50 000 as burn-in and thinned the remaining iterations at a rate of 10. We confirmed chain

convergence by visually inspecting traceplots and by calculating the Gelman–Rubin statistic (Gelman & Rubin, 1992), which was ≤1.1 for all chains in all models. We present coefficients of the covariate models as posterior mean, SD, 90% Bayesian credible intervals (BCI) and proportion of posterior samples above/below 0 ($p(\neq0)$). We used the 90% BCI, rather than the more commonly used 95% BCI, because its limits tend to be more stable (McElreath, 2018). For density and abundance estimates, we present the posterior mode and 90% Bayesian credible interval (BCI) because posterior distributions were right-skewed (the mean would be an overestimate of the location of the posterior and the SD would incorrectly imply symmetric uncertainty). A link to the data and code to fit all models can be found in the Data Availability statement below.

Results

The 22 surveys with suitable data for CMR analysis contained encounter histories for 624 individual crabs, of which 93 were recaptured at least once (Appendix S2, Table S1). For the remaining 53 surveys, capture numbers per sampling occasion ranged from 0 (11 surveys across nine sites) to 19; six sites (all surveyed only once) had no captures at all (Appendix S1, Table S1).

Coconut crab density

Estimates of density from the integrated model without covariates for the Chumbe lodge area (41.97 crabs/ha; 90% BCI: 31.93–55.92) (Table 1) were three times higher than the next site and much higher than elsewhere. Other sites had densities <10 crabs/ha, except for Manta Cave, Pemba Paradise (a hotel site) and Mapanya island, likely due to small search areas and few visits (Appendix S1, Table S1).

Abundance across suitable habitat

Site-level (i.e. subpopulation) abundance estimates across suitable habitat from posterior predictions ranged from 1.4 individuals (90% BCI: 0.33–23.95) on the small (2.7 ha) island of Hamisi to 2713.59 individuals (90% BCI: 1948.04–4762.20) on the 731-ha uninhabited island of Matumbini KP. Uncertainty for many abundance estimates was high (width of 90% BCI >> estimate) but decreased as the number of surveys at a site increased (Appendix S1, Figure S1). The total (meta-)population size of coconut crabs in the Pemba archipelago was estimated at 6687.97 individuals (90% BCI: 5050.58–10443.55).

Drivers of density

The strongest predictor of crab density ($p(\neq0) = 0.98$) was the presence of agriculture (Table 2); contrary to expectations, agriculture affected density negatively. Fishermen, hotels ($p(\neq0) = 0.96$) and government protection ($p(\neq0) = 0.91$) all affected density positively; for fishermen, this again went against our expectations. Effects of being on an

island or having nearby human settlements had less support (smaller coefficients, proportionally larger SD, $p(\neq0) \leq 0.87$).

Drivers of crab counts and body mass

The strongest predictors of counts per unit effort (with $p(\neq0) \geq 0.98$) were government protection (positive), presence of agriculture and settlements (both negative; Table 2). Analysing the body mass of 795 crabs caught across 23 sites, government protection was the strongest predictor ($p(\neq0) = 1$) and, as expected, affected body mass positively. The presence of hotels also affected body mass positively ($p(\neq0) = 0.91$; Table 2). Additional parameter estimates are provided in Appendix S1, Tables S3 (integrated model), S4 (counts) and S5 (body mass).

Discussion

We used an integrated model that leveraged spatially limited CMR data to estimate coconut crab subpopulation densities and sizes across 29 sites in and near the Pemba archipelago, many of which only had very sparse survey data. The resulting total metapopulation estimate suggests that the Pemba archipelago still sustains an important population of this species.

In the most westerly part of their range, coconut crabs have been mostly extirpated along continental coastlines from Somalia to Mozambique. Recent surveys of the Seychelles archipelago report that coconut crabs are rare (reviewed in Cumberlidge *et al*., 2022; Poupin *et al*., 2013); populations on the four main Comoro Islands have suffered rapid population declines of at least 50% over the past 15–20 years. Similarly, coconut crab populations on the Glorieuses Islands have declined by 80% over the past 15–20 years and, if present at all, are found only in very low numbers on military bases (Poupin *et al*., 2013). In the Mozambique Channel, coconut crabs are extremely rare on Juan de Nova Island and probably extirpated on Europa Island (Poupin *et al*., 2013). Coconut crabs are presumed exterminated from Madagascar based on exhaustive surveys. The species has also been eliminated from Mauritius (where it was reported to be declining by Charles Darwin in 1836) and it is absent from Reunion and Rodrigues (see Cumberlidge *et al*., 2022 for details). Nonetheless, the species still survives on Zanzibar (Caro *et al*., 2021).

Two small islands off the coast of Zanzibar are formally protected and renowned for their large coconut crab populations: Misali Island off the west coast of Pemba, and Chumbe Island off the south-west coast of Unguja (Fig. 1). Misali is largely undisturbed except for two temporary fishermen's camps, and currently has no hotels or villages; the Chumbe ecolodge, where crabs routinely feed on kitchen scraps, is known to sustain a high-density population. At least five previous studies across 14 years have been conducted on Misali, with population estimates ranging from 93 (Kassim, 2018) to 390 individuals (Merritt, 2014), with additional estimates of 239 (Harlan, 2014) and 157 (Klein & St. Denis, 2016). These numbers might indicate population

Table 2 Coefficient estimates (Est.) for covariates affecting density (D, crabs/ha), counts per unit effort (1 unit = 100 min in the field) and body mass (kg) of coconut crabs (*Birgus latro*) across 29 sites (23 with body mass information) in/near the Pemba archipelago, Tanzania. Estimates from integrated model of CMR and count data (density), negative binomial mixed model (counts) and linear mixed model (square root transformed body mass). Posterior mean (Estimate) and standard deviation (SD), lower (L) and upper (U) limits of 90% Bayesian credible interval (BCI), proportion of posterior samples above/below 0 ($p(\neq 0)$) and average model-predicted difference (Diff) in response variable between sites with and without the predictor (with standard error, SE)

Response	Predictor[a]	Est.	SD	L	U	p ($\neq 0$)	Diff (SE)
D	Agriculture	−1.14	0.54	−2.03	−0.32	0.98	−3.22 (2.25)
	Fishers	1.07	0.64	0.03	2.18	0.96	3.17 (2.34)
	Hotel	1.04	0.61	0.06	2.06	0.96	3.48 (3.07)
	Protection	1.04	0.76	−0.26	2.27	0.91	4.98 (5.85)
	Islands	−0.7	0.64	−1.77	0.41	0.87	−2.02 (2.1)
	Settlement	−0.34	0.61	−1.35	0.6	0.72	−0.90 (1.69)
Counts	Protection	1.04	0.36	0.48	1.65	1	4.44 (2.25)
	Agriculture	−0.61	0.3	−1.11	−0.12	0.98	−1.79 (0.98)
	Settlement	−0.59	0.28	−1.04	−0.12	0.98	−1.77 (0.93)
	Hotel	0.4	0.37	−0.19	1.02	0.87	1.09 (1.06)
	Fishers	0.37	0.35	−0.18	0.96	0.86	1.00 (0.99)
	Islands	0.1	0.34	−0.49	0.62	0.63	0.25 (0.91)
Body mass	Protection	0.25	0.07	0.13	0.36	1	0.43 (0.13)
	Hotel	0.1	0.07	−0.02	0.21	0.91	0.16 (0.12)
	Agriculture	−0.08	0.08	−0.21	0.04	0.87	−0.14 (0.12)
	Fishers	−0.07	0.07	−0.19	0.05	0.84	−0.12 (0.12)
	Islands	−0.03	0.08	−0.16	0.1	0.67	−0.06 (0.13)
	Settlement	0	0.08	−0.12	0.13	0.51	0 (0.12)

[a] Agriculture: Site with beans, maize or casava planted nearby; Fishers: Site with presence of fishermen camping overnight; Hotel: Site with unofficial protection offered within or near hotel grounds; Protection: site under government protection; Islands: site located on islands; Settlement: Site with nearby permanent settlements.

fluctuations over time, which is also suggested—for Misali and other CMR sites—by the considerable variation in survey-specific abundance estimates (Appendix S1, Table S6). However, abundance estimates from these previous studies are challenging to compare to our estimate of 214 individuals as they refer to undefined and likely varying sampled areas, as well as different amounts of time spent in the field. In the context of the Pemba archipelago, Misali harbours a considerable subpopulation of >200 individuals, with much larger subpopulations only occurring at sites which are *c.* 10 times greater in area (e.g. Fundo, Matumbini KP, Table 1).

Studies of coconut crabs on Chumbe have centred on the ecolodge, which attracts individuals, and extrapolation of lodge density to the entire island generates inflated abundance estimates: 1849 (Singh, 2010), 1761 (Roop, 2004), >1000 (Bruggers, 1999) and 354 (King, 2003). Even compared to Kilstromer & Bergwall (2013), who sampled across the island and estimated a population of 446 crabs, our island-wide estimate of 214 individuals is low. Our abundance estimate for the lodge area of 158 crabs (derived by multiplying lodge area density from the integrated model with the sampled area) is lower than the 291 individuals captured by Kilstromer & Bergwall (2013) in that area. But it is premature to attribute this to a declining population, rather than population fluctuations. For example, rangers on Chumbe report some seasonal fluctuations in crabs appearing at night around the kitchen area. Further, we could be underestimating the number of crabs in the northern and southern areas of the island, which is based on previously reported capture proportions (see Methods). Finally, our low estimates may in part be due to the choice of a 100-m buffer to define the sampled area, leading to a conservative density estimate.

Density in the Chumbe lodge area (42 crabs/ha), an area of provisioning, matched Christmas Island, Australia, with its high density of 16.3–47.3 crabs/ha (Drew & Hansson, 2014). With few exceptions, densities across subpopulations were <5 crabs/ha and thus much lower than on Aldabra, a protected island in the Seychelles, with an estimated average density of 23.7 crabs/ha (Appoo *et al.*, 2021). Accordingly, none of the Zanzibari sites, nor the entire Pemba archipelago, came close in population size to those reported for Christmas Island, with 1.257 million coconut crabs (Schiller, 1988), or Eastern Indian Ocean sites of Morotai Island and Sajafi Island in the Malaku Islands, Indonesia with 20 163 and 43 434 individuals respectively (Widiyanti, Marsoedi, & Setyohadi, 2016; Serosero *et al.*, 2021).

Body mass, densities and raw counts of coconut crabs at sites lacking formal protection were lower than on the four protected sites principally because no people other than rangers live permanently on those islands (see also Caro *et al.*, 2021). For density and body mass, informal protection offered by private hotels had similarly positive effects. Larval size and hence larval survival increase with female body mass and females only mate with males larger or equal in

size (Sato & Suzuki, 2010), so these results suggest that protection not only increases population density but also potential reproductive output. While the degree of connectivity among subpopulations through larval dispersal is unknown, this could point to protected subpopulations potentially serving as sources for the metapopulation. In contrast to findings from an earlier study (Caro *et al.*, 2021), however, we found negative effects of agriculture on crab densities and counts. This suggests that food supplements provided by local agriculture may not be important as formerly suggested or that their positive effects are counteracted by agriculture reducing the area of native coral rag forest where coconut crabs live. Also, against our expectations, the overnight presence of fishermen was positively related to density (and, weakly, counts) but we expect this is an artefact of small sample size.

Our data suggest the importance of government protection from exploitation and habitat encroachment. Consequently, there is an urgent need to give more formal protection to additional islands in the Zanzibari archipelago under the auspices of the Departments of Forestry and Fisheries responsible for conservation of biological resources on Zanzibar. Tourist lodges may bolster local crab densities by providing supplemental food resources (e.g. human food scraps) and halting hunting pressure due to non-consumptive values of tourists in the area. Whether this counters negative effects on population size due to habitat loss involved in hotel construction should be assessed in the future.

We derived an estimate of *c.* 6700 adult coconut crabs living on the Pemba archipelago. Although this figure does not match Indonesian sites of between 20 000 and 43 000 individuals, it still represents a substantial population in the Western Indian Ocean. In spite of its protection status, Misali has been leased for hotel development which is a great concern for this and other species inhabiting coral rag habitat. Other sites with large population sizes (e.g. Matumbini KP, Fundo, Ngao and Kokota) are also being leased for investment (Hamad *et al.*, 2023) which involves removing large areas of native vegetation for hotel construction, and an influx of people. We are hopeful that this metapopulation estimate, unusual for an invertebrate (Caro, 2022), can be used by departmental officials charged with conservation of Zanzibari wildlife to actively limit development of island sites and establish additional protected sites for this and other coral rag species.

Caveats

In addition to the assumptions described in the Methods section, our analysis also made strong assumptions about detection probability, movement and densities of coconut crabs. First, we used average detectability of crabs from five sites to inform detectability at sites without CMR surveys. Detection parameters varied among the five sites with CMR estimates. Using the same mean parameters for all non-CMR sites may inflate differences in density estimates among sites. Still, in the absence of data suitable for estimating site-specific parameters, average parameters from sites sampled

with the same field methods represents the best available information. Second, our decision to buffer all sampled areas by 100 m implies that crab movements are comparable across all sites. This may be violated if differences in ecological conditions across sites affect crab movements. Again, absence of site-specific movement information (and sparsity of movement information in general) precluded more nuanced buffering. In general, a more robust approach to density estimation, in which density does not depend on a subjectively chosen buffer, is preferable spatial capture–recapture modelling (SCR, Royle *et al.*, 2015). The approach also allows animal movement onto and off the search area, a violation of the geographic closure assumption in conventional CMR that was likely present at some sites. This requires recording spatial survey effort and capture locations of individuals and was not feasible in this study, but should be considered for future surveys. Models integrating SCR and other data types have been developed (e.g. Chandler & Clark, 2014) and could be adapted if SCR data can only be collected at a subset of sites. Thirdly, for some sites, the area to which we extrapolated population size was much larger than the sampled area. This entails the untested assumption that density is constant across large areas which almost certainly vary in their ecological conditions. Spatially replicated sampling on Misali suggests that there can be considerable variation in density even within a relatively small island (Appendix S1, Table S7). Therefore, ideally, these large areas should be further subsampled, and/or future sampling effort should be distributed across the archipelago so that ecological gradients potentially important for coconut crabs (e.g. nearby agriculture, distance from human settlements, etc.) are well represented and relationships between ecological conditions and density can be estimated.

Metapopulation survey recommendations

While integrating information from data-rich and data-poor sites allowed estimation of abundance for the latter, these estimates come with high uncertainty, which, in turn, affects uncertainty of the metapopulation estimate. Several of the data-poor subpopulations in this study had extremely few (and possibly no) crabs, and repeated visits to such unproductive sites, especially when remote, may be hard to justify. At the same time, the return on investment – in terms of gains in precision with increased effort – declines at high effort (Appendix S1, Figure S1).

How to allocate limited effort across subpopulations depends on project objectives. If the goal is to determine the extent and size of a metapopulation, all potentially occupied sites need surveying. A similar argument applies to monitoring over time if the goal is to understand extinction/colonisation dynamics which will probably occur in small subpopulations. In that case, allocating more than a single visit to all sites to improve precision is advisable. If the objective is enumerating/monitoring the bulk of individuals, unproductive sites could be dropped and effort better distributed equitably among remaining subpopulations. In this case,

data imbalance among sites was extreme, and some degree of standardization of sampling across the metapopulation is likely advisable. Additionally, even single visit surveys could be made more useful if additional information on detectability was collected (e.g. using double observer sampling; Royle, 2004b). Principles of large-scale monitoring designs that balance spatial extent and temporal replication (e.g. panel designs in which some locations are visited every year, whereas others are visited at longer time intervals; Urquhart & Kincaid (1999)) could be used to determine optimal sampling strategies for a specific study objective.

Broader significance

Our study shows how relatively meagre subpopulation data can be used to estimate the size of highly fragmented populations, something often dismissed as being too difficult in conservation science studies. Nevertheless, the behaviour of populations in fragmented habitats is central to conservation science and practice (Fahrig, 2003; Haddad *et al*., 2015). It is seen in the context of piecemeal habitat destruction which occurs during the advance of small-scale agriculture into pristine habitat, land division caused by road networks, urban sprawl into rangeland and poorly planned habitat restoration projects. Fragmentation also bedevils populations in nature reserves isolated from each other by agriculture, and in natural populations living in isolated lakes, mountain top habitats, or island archipelagos. Irrespective of whether these fragmented populations are connected or not, our ability to estimate their sizes across these landscapes will make conservation plans better informed and relevant.

Acknowledgements

Author contributions

TC conceived of the study and sampled crabs in all the sites, many with RSR. JZ conducted research on Misali. L-MG conducted research on Chumbe. RS analysed the data. TC and RS wrote the paper.

Conflict of interest

The authors have no conflict of interest.

Data availability statement

Data and code to replicate the presented analyses can be downloaded from Zenodo (https://doi.org/10.5281/zenodo.8153309).

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Additional data and model results.

Table S1. Details of surveys of coconut crabs (*Birgus latro*) across 29 sites in/near the Pemba archipelago, Tanzania.

Table S2. Site-specific total area of suitable habitat (Hab., ha), summary of survey effort (SV = number of surveys, YR = number of years with surveys), and binary covariates used to model coconut crab (*Birgus latro*) density across 29 sites in/near the Pemba archipelago, Tanzania, and (below) total number of sites with presence of each binary covariate.

Table S3. Posterior mean, standard deviation (SD), lower (L) and upper (U) limits of 90% Bayesian Credible Interval (BCI) of detection parameters and parameters describing variation in expected abundance from the integrated model of capture-mark-recapture (CMR) and N-mixture data for coconut crabs (*Birgus latro*) across 29 sites in/near the Pemba archipelago, Tanzania.

Table S4. Posterior mean, standard deviation (SD), lower (L) and upper (U) limits of 90% Bayesian Credible Interval (BCI) of the negative binomial mixed models (one per binary predictor variable) fit to survey-level counts of coconut crabs (*Birgus latro*) across 29 sites in/near the Pemba archipelago, Tanzania. b0 = intercept (log-scale); r = negative binomial overdispersion; SD.eps = standard deviation of normal site random effect.

Table S5. Posterior mean, standard deviation (SD), lower (L) and upper (U) limits of 90% Bayesian Credible Interval (BCI) of the linear mixed models (one per binary predictor variable) fit to square root transformed weights of coconut crabs (*Birgus latro*) across 23 sites in/near the Pemba archipelago, Tanzania. b0 = intercept; b.sex = effect of being female; mu.s, sig.s = mean and SD of normal random effect for log(site-level residual SD).

Table S6. Posterior mode (N), lower (L) and upper (U) limits of 90% Bayesian Credible Interval (BCI) of survey-specific coconut crab abundance for sites with repeated CMR surveys from the integrated model of capture-mark-recapture (CMR) and N-mixture data for coconut crabs (*Birgus latro*) across 29 sites in/near the Pemba archipelago, Tanzania.

Table S7. Posterior mode (N), lower (L) and upper (U) limits of 90% Bayesian Credible Interval (BCI) of survey-specific coconut crab (*Birgus latro*) density (crabs/ha) from CMR surveys conducted on 4 transects (TC and JZ1 overlap) on Misali in winter 2022, estimated within the integrated model of capture-mark-recapture (CMR) and N-mixture data for coconut crabs across 29 sites in/near the Pemba archipelago, Tanzania.

Figure S1. Width of 90% Bayesian Credible Interval (BCI) of site-level abundance estimates of coconut crabs (*Birgus latro*), divided by abundance estimate, plotted against the total number of nightly visits to each site, for 29 sites in/near the Pemba archipelago, Tanzania.

Appendix S2. Preliminary CMR analyses to determine detection model structure.

Table S1. Details of coconut crab (*Birgus latro*) surveys included in capture-recapture models (#cap = number of individuals captured; #recap = number of individuals recaptured at least once).

Table S2. AIC scores for different detection models (for model definition see text above) fit to coconut crab (*Birgus latro*) capture-recapture data from 5 sites in/near the Pemba archipelago, Tanzania, with difference to top model (ΔAIC) and number of model parameters (npar).