

## Chapter 22

# Geographic variation in reproduction and survival of Kelp Gulls *Larus dominicanus vetula* in southern Africa

Res Altwegg<sup>1\*</sup>, Robert J.M. Crawford<sup>1,2</sup>, Les G. Underhill<sup>1</sup>, A. Paul Martin<sup>3</sup> and Philip A. Whittington<sup>4</sup>

<sup>1</sup> Avian Demography Unit, Department of Statistical Sciences, University of Cape Town, Rondebosch 7701, South Africa

<sup>2</sup> Marine & Coastal Management, Department of Environmental Affairs & Tourism, Private Bag X2, Rogge Bay 8012, South Africa

<sup>3</sup> 30 Himeville Drive, Bluewater Bay 6210, South Africa

<sup>4</sup> Department of Zoology, P.O. Box 77000, Nelson Mandela Metropolitan University, Port Elizabeth 6031, South Africa

\* Corresponding author, e-mail: altwegg@adu.uct.ac.za

Different populations of a species tend to vary in survival and reproduction, but the extent and scale of such spatial variation are poorly known. We estimated survival and clutch size of Kelp Gulls (*Larus dominicanus vetula*) across their entire African range. At this large geographic scale, we found no evidence for spatial variation in survival, and there was no variation in clutch size. However, there was considerable variation in clutch size among colonies within regions. Over the whole study, mean annual survival of juvenile and adult birds was 0.44 and 0.84, and mean clutch size was 2.2 eggs. A matrix

population model showed that population growth was least sensitive to variation in clutch size, and the observed variation in clutch size could not fully account for the observed variation in population growth among colonies and regions. Our results thus suggest that dispersal and/or variation in survival (including egg/nestling survival) at a small spatial scale are also important for the spatial pattern of Kelp Gull population dynamics. These results are consistent with a metapopulation approach to spatial population dynamics.

**Keywords:** capture–mark–recapture, demographic variation, matrix population model, metapopulation dynamics, spatial fitness variation

### Introduction

Survival and reproduction can vary among populations as much as among species (Dhondt 2001). At the scale of metapopulations, such demographic variation can result in net increases in some populations and decreases in others (Ringsby *et al.* 1999, 2002, Sæther *et al.* 1999). Demographic variation among populations at a larger scale, across the geographic distribution of a taxon probably is also significant, but has rarely been investigated (e.g. Blondel *et al.* 1992, Harris *et al.* 2005). Recently, Frederiksen *et al.* (2005a) found considerable variation in demography and dynamics among populations of kittiwakes *Rissa tridactyla* across their range in the northern Atlantic and Pacific. It is currently unknown, whether such large-scale variation in demography is the rule or the exception among birds and other animals. Here we examine survival and reproduction of Kelp Gulls *Larus dominicanus vetula* across their African range.

Kelp gulls *Larus dominicanus* have a wide distribution in the southern hemisphere, including southern Africa (Croxall 1984, 1991, Higgins and Davies 1996, Hockey *et al.* 2005). The race, *L. d. vetula* is endemic to southern Africa (Brooke and Cooper 1979), except for a few birds that bred north of the equator in Senegal in 1998 (Keijl *et al.* 2001). Other than that, *L. d. vetula* breeds from Isla dos Tigres, southern Angola to Hamburg in South Africa's Eastern Cape Province (Dean *et al.* 2002, Hockey *et al.* 2005, A.J. Tree in litt.).

South Africa is home to the largest part of the *L. d. vetula* population: in 1976–1981, there were 7650 pairs in the Western Cape province, and 1100 in the Eastern Cape province (Crawford *et al.* 1982). Namibia had an additional 2300 pairs at that time (Crawford *et al.* 1982). Since then, the overall population of *L. d. vetula* increased from about 11 200 pairs to 22 500 pairs or more in 2000 (Hockey *et al.* 2005, who also include a distribution map). The mean annual population growth rate was thus ~3% ( $\lambda = 1.033$ ). These population increases were accompanied by a probable range expansion into southern Angola (Dean *et al.* 2002). Over the same time, populations increased at nine colonies in the Western Cape from 6 500 to 17 900 pairs (Steele and Hockey 1990, Hockey *et al.* 2005), which corresponds to a mean annual population growth rate  $\lambda = 1.049$ . Likewise, the Kelp Gull population in the Eastern Cape as a whole increased at  $\lambda = 1.022$  since 1982, but individual colonies increased, decreased or stayed constant (Whittington *et al.* 2006).

These observations suggest spatial variation in Kelp Gull population dynamics at several scales. Kelp gulls in southern Africa thus offer an excellent opportunity to study spatial variation in demography and to examine to what extent such variation may have led to differences in local population dynamics. At the largest scale, we distinguish three geographic regions, Namibia, Western Cape and Eastern Cape. The Namibian colonies are separated from those in the Western Cape by ca. 500 km of coastline where only few

Kelp Gulls breed (150 pairs, Crawford *et al.* 1982). The colonies in Western and Eastern Cape are closer to each other, but ring recoveries suggest that there is nevertheless little movement between these two regions (Underhill *et al.* 1999). Within these regions, we examined variation among colonies. Ringing recoveries suggest that there is little movement of fledglings away from their natal colonies, as 75% of birds ringed as chicks and recovered at ages five years and older were within 18 km of their place of ringing (Underhill *et al.* 1999). The rapid increase in Kelp Gull numbers over the last decades indicates that the populations were below their carrying capacities at least until the recent past and we can use simple density-independent population models to describe their dynamics.

Kelp Gull populations were controlled at guano islands until the early 1960s, mainly through egg and chick destruction (Crawford *et al.* 1982, Randall *et al.* 1981). At some localities, control continued until 1978 (Crawford *et al.* 1982). Kelp Gull populations may thus still be recovering from these control measures, but supplementary food made available by human activities is probably also an important factor in the increases (Steele 1992, Steele and Hockey 1990). The population densities are now so high that control measures were recently reintroduced at two Namibian islands (Hockey *et al.* 2005).

A second goal of this study is to provide critical information for management plans. Both conservation and control efforts tend to be most effective if they target a life stage that has the greatest effect on population dynamics (Caswell 2001, Govindarajulu *et al.* 2005). Yet, culling programmes implemented by management agencies have not always taken account of all factors responsible for the population dynamics of colonies and the effects of culls (Bosch *et al.* 2000). The construction of demographic models can assist in the consideration of such factors and hence in better decisions. For example, models have suggested that limiting reproductive effort can be an effective method of control for certain species of gull but not for others (Wanless *et al.* 1996).

## Methods

Adult Kelp Gulls were mostly caught in walk-in traps placed over the nest, and incidentally in mist nets targeting other species. Juveniles were caught and ringed prior to fledging. Regular checks were kept for breeding at known breeding sites, and nests were counted and their content recorded as close as possible to the period when breeding activity was at its peak.

We estimated survival of Kelp Gulls along the southern African coast using two independent data sets. The first data set included 10 059 individuals ringed at ca. 60 sites along the coast of Namibia and South Africa between 1990 and 2004; the second data set included 75 adult individuals ringed and observed at Lambert's Bay in the Western Cape between October 1999 and January 2006. We treated the data sets separately because they differed in their quality. The birds in the first data set were ringed with a numbered metal ring, whereas the birds in the second data set additionally received a plastic ring on which a unique combination of two letters or numbers could be read from a distance with the use of binoculars. The first data set therefore consisted of recaptures of live birds and recoveries of dead birds, whereas the second consisted of resightings and recaptures of live birds (391 resightings and recaptures of 75 individuals in total).

We were interested in finding possible large-scale geographic variation in survival and therefore divided the first data set along the coastline into three regions, motivated by

the near-discrete breeding populations: Namibia, Western Cape, and Eastern Cape. In Namibia, the data comprised 2270 individuals ringed as juveniles and 14 ringed as adults; 10 were later recaptured alive at least once and 51 were found dead. In the Western Cape, 4265 individuals were ringed as juveniles and 246 as adults; 37 were recaptured at least once and 123 were found dead. In Eastern Cape, 3240 juveniles and 38 adults were ringed; 17 were recaptured at least once and 169 were found dead. The individuals that were either recaptured or recovered had moved 0 to 1169 km between encounters, but only 24 individuals moved from one region to another. First-year birds usually disperse away from breeding colonies. In South Africa, 60% of birds may not return to natal islands until they are aged two years. Three-year-old birds have visited non-natal colonies, but breeders have all nested at natal colonies (Crawford *et al.* 2000). However, the recent establishment of several new colonies means some birds must settle at non-natal colonies or breed at a different colony from the one where they first bred (e.g. Calf *et al.* 2003, Whittington *et al.* 2006).

We analysed the first data set using combined live-recapture and dead-recovery models (Brownie *et al.* 1985, Burnham 1993, Lebreton *et al.* 1992), implemented in program MARK (White and Burnham 1999). These models allow separating true survival from the probability of recapturing a live individual (referred to as recapture rate) and the probability that a dead individual is found and reported (referred to as recovery rate). These models also estimate fidelity, the probability of staying at the study site, because recoveries can be made outside the study area. In our case, ringing activity was not confined to a restricted area, and we interpret the fidelity rates therefore as movement away from the ringing locations. Different causes of death could have determined whether a bird dies at the ringing locations or somewhere else, and would thus have affected the fidelity rates, as would heterogeneity in recapture probability.

We examined differences in survival, recapture, recovery and fidelity between young gulls (first year of their life) and older ones. We expected the age effects to be largest between first year gulls and older ones, but we also examined a model allowing for full age dependence in survival up to four years when Kelp Gulls start breeding (Crawford *et al.* 2000). A third model held survival constant for 1- to 3-year-old immature birds.

We examined differences in all model components among the three regions, but the data were too sparse to examine temporal variation. Our most general model therefore included interactive effects of age and region on all four model components. Then we simplified each component in turn and evaluated the models using the sample size adjusted Akaike's Information Criterion (AICc, Burnham and Anderson 2002).

The methods we used assume that all individuals within a group have the same survival, recapture, recovery, and fidelity rates. We examined how closely the data met these assumptions for our most general model (Model 5, Table 1) using the median c-hat approach implemented in program MARK (White and Burnham 1999). Using 20 replicated simulations at 12 levels of overdispersion between 1 and 2, this procedure estimated c-hat at 1.52 (se = 0.01). A second method to estimate goodness-of-fit, the parametric bootstrap procedure in program MARK, yielded a slightly higher estimate of c-hat (1.64, based on 200 simulations, comparing deviances), but is known to overestimate c-hat when the data are sparse (White 2002). These estimates of c-hat indicate that the model structurally fits the data, but that there is some heterogeneity among individuals. We therefore used the c-hat obtained by the first approach and based model selection on Quasi-likelihood Akaike's Information Criterion,

QAICc (Anderson *et al.* 1994). Our results do not depend on the choice between these two estimates of  $c$ -hat.

The second data set consisted of resightings and recaptures of live gulls, and we used ordinary capture–mark–recapture models to estimate survival and recapture rates (Lebreton *et al.* 1992). This data set allowed us to examine variation in survival and recapture over the years, in addition accounting for differences in recapture between breeding seasons and non-breeding seasons. Using identical procedures for estimating  $c$ -hat as above, we found no evidence of overdispersion in the second data set and therefore made no adjustments ( $c$ -hat = 0.896,  $se = 0.076$ ).

Eleven colonies in Namibia, eight colonies in the Western Cape, and six colonies in the Eastern Cape were visited once a year during the peak breeding season (10 October to 13 December) for one to nineteen years between 1985 and 2004. During these surveys, all nests were counted and their contents recorded. Here we concentrate on the nests that contained at least one egg. The number of eggs (or eggs plus downy chicks) was taken as a measure of brood size. Clutch sizes ranged from one to five eggs, or one egg and one to two downy chicks. The clutches with more than three eggs could possibly have been laid by two females (Hockey *et al.* 2005), but excluding those nests ( $n = 43$  of  $n = 14995$  in total) did not change our results.

We partitioned the variance in clutch size into three components, within colony, among colonies, and among the three geographic regions. For this we used a generalized linear mixed model with Poisson errors and a log link function implemented in procedure `glmmPQL` in program R 2.2.1 (Venables and Ripley 2002, R Development Core Team 2003). We added year as a fixed effect, and time of the season (days since 1 October) as a covariate to the model to account for potential variation in clutch sizes caused by these factors. Laying occurs from late September to January, with replacement eggs laid into February (Hockey *et al.* 2005).

We illustrate the effect of variation in demography on population growth rates using a simple matrix population model. Assuming a post-breeding census and a one-year projection interval, we project the number of individuals in year  $t + 1$  from the number of individuals in year  $t$ :

$$n_{t+1} = An_t, \quad \text{eqn. (1)}$$

where  $n$  is a vector with the number of individuals in each age-class, and  $A$  is the projection matrix:

$$A = \begin{pmatrix} 0 & 0 & 0 & c * s_n * s_a * 0.5 \\ s_y & 0 & 0 & 0 \\ 0 & s_i & 0 & 0 \\ 0 & 0 & s_i & s_a \end{pmatrix} \quad \text{eqn. (2)}$$

The matrix elements are survival of first-year birds ( $s_y$ ), immature birds ( $s_i$ ), and adult birds ( $s_a$ ), and reproduction, which is the product of clutch size ( $c$ ), nestling survival ( $s_n$ ), adult survival and sex ratio (assumed to be 0.5). For *L. d. vetula*, the age at first breeding is four years (Crawford *et al.* 2000), and we assumed that adult individuals breed every year. Our study yielded estimates for all of these variables except nestling survival (survival from the time the nests were censused until the young gulls reached a size at which they could be ringed). Therefore, we chose a value of nestling survival that produced the mean observed population growth rate of Kelp Gulls in southern Africa over the last 30 years.

Assuming a stable age distribution, the dominant eigenvalue of  $A$  gives the population growth rate ( $\lambda$ ), and the sensitivity of  $\lambda$  to changes in each matrix element shows how

much population growth is affected by variation in each fitness component (Caswell 2001). We conducted all matrix analyses in program R 2.2.1 (R Development Core Team 2003).

## Results

For the first capture–recapture data set, model selection favoured a model allowing for differences in recapture, recovery and fidelity rates among the areas (Model 1, Table 1). This model further implied that survival and fidelity differed between the first-year birds and older ones (Figure 1). The best model was almost twice as likely as the second best model, which allowed for variation in survival over three age-classes (Model 2, Table 1; ratio of QAICc weights: 0.46/0.25 = 1.84). According to the best model, juvenile survival was 0.44 (95% confidence interval: 0.35 to 0.54) and adult survival 0.84 (0.77 to 0.89) over the whole area of our study (i.e. nearly the whole range in Africa). The probability of recapturing a live individual was 0.234 (0.085 to 0.501) in Namibia, 0.013 (0.006 to 0.031) in the Western Cape, and 0.003 (0.001 to 0.006) in the Eastern Cape. The probabilities of finding and reporting a dead individual were 0.027 (0.019 to 0.038) in Namibia, 0.039 (0.030 to 0.050) in the Western Cape, and 0.064 (0.051 to 0.077) in the Eastern Cape. The fidelity rates were 0.023 (0.008 to 0.063) and 0.740 (0.397 to 0.925) for Namibian juveniles and adults, and 0.608 (0.130 to 0.942) and 0.995 (0.920 to 0.999) for juveniles and adults in the Western Cape. In the Eastern Cape, there was hardly any emigration even though we could not obtain a reliable estimate for juveniles (1,  $se = 0.00003$  for adults).

For the second data set, model selection favoured a model with constant survival and time dependent recapture probabilities (best model: Deviance = 331.08, number of parameters,  $K = 13$ , AICc = 715.03; model with time dependent survival:  $\Delta AICc = 4.67$ ; model with constant recapture:  $\Delta AICc = 10.21$ ). Annual adult survival at Lambert's Bay between 1999 and 2006 was 0.84 (95% CI: 0.78 to 0.89) and thus identical to the mean estimate for rest of the range. The recapture rates at Lambert's Bay varied over time from 0.19 (0.09 to 0.37) to 0.64 (0.48 to 0.78).

Clutch size varied significantly from year to year ( $F_{18,14951} = 25.72$ ,  $P < 0.001$ ), and increased slightly (slope on log scale: 0.001; i.e. ca. 0.1% per day) through the season ( $F_{1,14951} = 4.509$ ,  $P = 0.034$ ), and we therefore left these fixed effects in the model when estimating the spatial variance. Of the remaining variance, most was due to variation among nests within colonies ( $var = 0.221$ ), less due to variation among colonies nested within region ( $var = 0.0061$ ), and almost nothing due to variation among regions ( $var = 1.6 \times 10^{-9}$ ). Our data were insufficient to examine whether the temporal pattern was similar among colonies or regions (*sensu* Frederiksen *et al.* 2005b). We compared the colonies in 1995, when 15 of the 25 colonies were counted, based on the best linear unbiased predictors (BLUP) of the random effects (colony nested within region). In that year, estimated mean clutch size varied between 1.87 at Meeuw Island in the Western Cape and 2.37 at Penguin Island in Namibia, around a mean of 2.12 (the mean over the whole study period was 2.20). There was no significant correlation between mean clutch size and colony size ( $r = 0.20$ ,  $N = 25$ ,  $P = 0.33$ ).

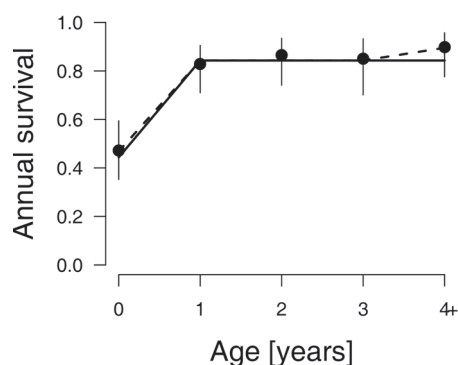
We used a simple matrix population model (equations 1 and 2) to examine population level consequences of the estimated survival rates and clutch size. This model requires also an estimate of egg/nestling survival between the time of the nest censuses and the age at which young gulls generally were ringed, immediately prior to fledging. We could not get such an estimate directly. However, with a mean

**Table 1:** Summary of model selection for Kelp Gull survival in Southern Africa. The models are combined mark–recapture and dead-recovery models. They consist of four parts modelling survival (S), recapture (P), recovery (r), and fidelity (F) rates. The subscripts denote the factors affecting a particular rate. We considered the effect of age (age2: first-year birds vs older; age3: juveniles, immatures, adults; age5: full age dependence up to age 4 years) and area (Namibia, Western Cape, and Eastern Cape) on each of the model components. Additive effects are denoted by '+', interactive effects by '\*'. Constant model components are denoted by '.'. The models are sorted according to their Quasi-likelihood Akaike's Information Criterion (QAICc), where a lower value indicates a better model. Delta QAICc is the difference in QAICc between the current and the best model; QAICc weights give the relative support each model has compared to the other ones in the set; K is the number of parameters; and QDeviance is the model deviance divided by the variance inflation factor  $\hat{c}$ , which was 1.52

| Model  | QAICc    | Delta QAICc | QAICc weights | K  | QDeviance |
|--|----------|-------------|---------------|----|-----------|
| 1) $S_{age2} P_{area} r_{area} F_{age2+area}$                | 3098.092 | 0.000       | 0.463         | 12 | 511.102   |
| 2) $S_{age3} P_{area} r_{area} F_{age2+area}$                | 3099.288 | 1.196       | 0.254         | 13 | 508.973   |
| 3) $S_{age2+area} P_{area} r_{area} F_{age2+area}$           | 3100.205 | 2.113       | 0.161         | 14 | 509.204   |
| 4) $S_{age2+area} P_{area} r_{.} F_{age2+area}$              | 3101.727 | 3.634       | 0.075         | 12 | 514.736   |
| 5) $S_{age5} P_{area} r_{area} F_{age2+area}$                | 3102.736 | 4.643       | 0.045         | 15 | 508.408   |
| 6) $S_{age2+area} P_{area} r_{area} F_{age2}$                | 3110.020 | 11.928      | 0.001         | 12 | 523.029   |
| 7) $S_{age2*area} P_{age2*area} r_{age2*area} F_{age2*area}$ | 3115.430 | 17.338      | 0.000         | 24 | 504.350   |
| 8) $S_{age2+area} P_{area} r_{area} F_{area}$                | 3119.232 | 21.139      | 0.000         | 13 | 530.236   |
| 9) $S_{age2+area} P_{.} r_{area} F_{age2+area}$              | 3124.561 | 26.469      | 0.000         | 12 | 537.574   |

clutch size of 2.20 and the best estimates for juveniles, immatures and adults, nestling survival would have had to be 0.74 for the model to produce the observed mean population growth rate  $\lambda = 1.033$ . At these parameter values, the model suggests that Kelp Gull population dynamics are most sensitive to changes in adult survival (sensitivity: 0.64), less sensitive to changes in juvenile survival (0.28) and reproduction (0.18), and least sensitive to changes in immature survival (0.15).

This model also allowed us to explore the potential effect of the observed variation in clutch size among colonies on population growth. The observed variation could have led to variation in the population growth rate  $\lambda$  ranging from 1.018 to 1.048. While this is a considerable amount of variation (corresponding to population doubling times between 38 and 15 years), variation in clutch size alone cannot account for all the observed variation in population growth among colonies (some colonies decreased, Whittington *et al.* 2006).



**Figure 1:** Age-specific survival of Kelp Gulls in Southern Africa. Dots and vertical lines show the maximum likelihood estimates and their 95% confidence intervals taken from the model with full age dependence up to age 4 years (Model 5, Table 1). The solid line shows the best model (Model 1, Table 1), and the dashed line shows the second best model (Model 2, Table 1)

## Discussion

We estimated survival and clutch size of Kelp Gulls across their entire range in southern Africa, and examined spatial variation in these demographic rates. We found no evidence for spatial variance in survival, and there was no variance among regions in clutch size. However, there was considerable variance in clutch size among colonies within regions. Kelp gull populations increased in southern Africa over the last 30 years, and the rate of increase varied among regions and colonies, with a few colonies even decreasing (Whittington *et al.* 2006). Using a simple matrix population model, we found that the observed variation in clutch size could not account for all of this variation in population growth. There may have been variation in survival (including nestling survival) among colonies, but we did not have sufficient data to examine variation at this scale. Our results suggest that most of the spatial variance in demography was at the among-colony level, and very little at a larger inter-regional level. Our results are consistent with the metapopulation paradigm focusing on variation among local populations that are connected through dispersal, (Hanski 1998, Hanski and Gilpin 1997). Our results are also consistent with Harris *et al.* (2005), who found no spatial variation in survival of Atlantic puffins (*Fratercula artica*), but they are in contrast to a recent study showing large-scale variation in demography of kittiwakes *Rissa tridactyla* across the north Atlantic and Pacific oceans (Frederiksen *et al.* 2005a).

Our survival estimate of 0.84 for adult Kelp Gulls is the first such estimate for this species, and is somewhat lower than comparable estimates for the closely related gulls *Larus fuscus* and *L. argentatus*, for which survival rates around 0.9 were reported (Wanless *et al.* 1996). Our mean estimate of clutch size (2.20) is close to earlier estimates for Kelp Gulls in South Africa (2.1, 2.1, and 2.2, Calf *et al.* 2003, Crawford *et al.* 1982, Williams *et al.* 1984). A Kelp Gull population in Wellington, New Zealand (*L. d. dominicanus* subspecies), had a mean clutch size of 2.4, and 1.3 young per breeding pair reached the flying stage (Fordham 1964). Nestling survival was therefore lower in that study (0.54) compared to our indirect estimate of 0.74. On the other hand, in a newly established colony in South Africa nestling survival was 0.88

(Calf *et al.* 2003). In Golfo San Jorge, Patagonia, mean clutch sizes were 2.3 and 2.5 in two different years (Yorio and Garcia Borboroglu 2002). Further south, Kelp Gull clutch sizes were 1.9 on the subantarctic Marion Island (Williams *et al.* 1984), and 2.6 near Palmer Station on the Antarctic Peninsula (Parmelee *et al.* 1977). Even at this very large spatial scale and across two subspecies, clutch size thus seems to vary little more than among colonies in South Africa. We probably slightly underestimated clutch size because some of the clutches may have been incomplete at the time of the census. However, the laying interval in Kelp Gulls is short (2.5 days) compared to the incubation period (26–27 days, Williams *et al.* 1984) so that this bias would have been small. Although there is substantial dispersal of adult Kelp Gulls away from some breeding colonies in the Western Cape (Crawford *et al.* 1997, but see Underhill *et al.* 1999), the high fidelity rate estimated for these birds suggests they remain mainly within the regions considered (Namibia, Western Cape, Eastern Cape). First-year Kelp Gulls had much lower fidelity rates than older birds, implying that they undertake longer movements, as also indicated by recoveries and resightings of banded birds (Underhill *et al.* 1999). Heterogeneity in recapture rates may also have lowered the fidelity estimates (Frederiksen, pers. comm.).

Kelp gull populations in Namibia have increased to a point where population control is being resumed again. In addition to the discontinued control efforts (Crawford *et al.* 1982) and supplementary food from offal (Steele and Hockey 1990), which probably increased survival, birds may also breed at a younger age now than in earlier years. In New Zealand, birds of the nominate race *dominicanus* may breed when aged three years, but most breed for the first time when four years old (Fordham 1964, Higgins and Davies 1996). In South Africa, one of 11 known-aged birds may have bred three years old, but 50–80% of birds aged four years and all older birds bred (Crawford *et al.* 2000). In the Eastern Cape, however, some individuals acquire full adult plumage at 2–3 years and one known aged bird bred at the age of three (PAW pers. obs., SAFRING, unpublished data). Even though we cannot identify the cause of the observed population increases, our matrix model showed that Kelp Gull population growth was most sensitive to changes in adult survival. Conservation and management efforts for this species would thus potentially have the highest impact if they targeted the adult life stage.

*Acknowledgements* – Data collection was coordinated by SAFRING. RA and PAW were supported by the South African National Research Foundation (NRF). LGU acknowledges support from the Sea and Shore 2 programme of the NRF. We also acknowledge our respective institutions for support. We thank M.G. Boorman, B.L. Dundee and staff of Ministry of Fisheries and Marine Resources, Namibia for banding Kelp Gulls in Namibia. We are grateful to B.M. Dyer, L. Upfold, V.L. Ward and others who assisted with the banding and resighting of Kelp Gulls in South Africa, and to Morten Frederiksen, Theunis Piersma and an anonymous reviewer for comments on the manuscript. This paper is a contribution of Project LMR/EAF/03/02 of the Benguela Current Large Marine Ecosystem (BCLME) Programme.

## References

- Anderson, D.R., Burnham, K.P. and White, G.C. 1994. AIC model selection in overdispersed capture–recapture data. *Ecology* 75: 1780–1793.
- Blondel, J., Pradel, R. and Lebreton, J.-D. 1992. Low fecundity insular blue tits do not survive better as adults than high fecundity mainland ones. *J. Anim. Ecol.* 61: 205–213.
- Bosch, M., Oro, D., Cantos, F.J. and Zabala, M. 2000. Short-term effects of culling on the ecology and population dynamics of the yellow-legged gull. *J. Appl. Ecol.* 37: 369–385.
- Brooke, R.K. and Cooper, J. 1979. The distinctiveness of southern African *Larus dominicanus* (Aves: Laridae). *Durban Museum Novitates* 12: 27–37.
- Brownie, C., Anderson, D.R., Burnham, K.P. and Robson, D.S. 1985. Statistical inference from band recovery data – a handbook. US Fish and Wildlife Service, Resource publication 156. 2nd edition.
- Burnham, K.P. 1993. A theory for combined analysis of ring recovery and recapture data. In: Lebreton, J.-D. and North, P.M. (eds). *Marked individuals in the study of bird populations*. Birkhäuser Verlag, Basel. pp. 199–213.
- Burnham, K.P. and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information–theoretic approach. Springer.
- Calf, K.M., Cooper, J. and Underhill, L.G. 2003. First breeding records of kelp gulls *Larus dominicanus vetula* at Robben Island, Western Cape, South Africa. *Afr. J. Marine Sci.* 25: 391–393.
- Caswell, H. 2001. Matrix population models. Sinauer.
- Crawford, R.J.M., Cooper, J. and Shelton, P.A. 1982. Distribution, population size, breeding and conservation of the Kelp Gull in southern Africa. *Ostrich* 53: 164–177.
- Crawford, R.J.M., Dyer, B.M. and Upfold, L. 2000. Age at first breeding and change in plumage of kelp gulls *Larus dominicanus* in South Africa. *S. Afr. J. Marine Sci.* 22: 27–32.
- Crawford, R.J.M., Nel, D.C., Williams, A.J. and Scott, A. 1997. Seasonal patterns of abundance of Kelp Gulls *Larus dominicanus* at breeding and non-breeding localities in southern Africa. *Ostrich* 68: 37–41.
- Croxall, J.P. 1984. Status and conservation of the world's seabirds. ICBP.
- Croxall, J.P. 1991. Seabird status and conservation: a supplement. ICBP.
- Dean, W.R.J., Dowsett, R.J., Sakko, A. and Simmons, R.E. 2002. New records and amendments to the birds of Angola. *Bull. Brit. Ornithol. Club* 122: 180–185.
- Dhondt, A.A. 2001. Trade-offs between reproduction and survival in tits. *Ardea* 89: 155–166.
- Fordham, R.A. 1964. Breeding biology of the southern black-backed gull: II: incubation and the chick stage. *Notornis* 11: 110–126.
- Frederiksen, M., Harris, M.P. and Wanless, S. 2005a. Inter-population variation in demographic parameters: a neglected subject? *Oikos* 111: 209–214.
- Frederiksen, M., Wright, P. J., Harris, M. P., Mavor, R. A., Heubeck, M. and Wanless, S. 2005b. Regional patterns of kittiwake *Rissa tridactyla* breeding success are related to variability in sandeel recruitment. *Mar. Ecol. Progr. Ser.* 300: 201–211.
- Govindarajulu, P., Altwegg, R. and Anholt, B.R. 2005. Matrix model investigation of invasive species control: bullfrogs on Vancouver Island. *Ecol. Appl.* 15: 2161–2170.
- Hanski, I. 1998. Metapopulation dynamics. *Nature* 396: 41–49.
- Hanski, I. and Gilpin, M.E. 1997. Metapopulation dynamics: ecology, genetics, and evolution. Academic Press.
- Harris, M.P., Anker-Nilssen, T., McCleery, R.H., Erikstad, K.E., Shaw, D.N. and Grosbois, V. 2005. Effect of wintering area and climate on the survival of adult Atlantic puffins *Fratercula arctica* in the eastern Atlantic. *Mar. Ecol. Progr. Ser.* 297: 283–296.
- Higgins, P.J. and Davies, S.J.J.F. 1996. Handbook of Australian, New Zealand & Antarctic birds. Volume 3 Snipe to pigeons. Oxford University Press.
- Hockey, P.A.R., Dean, W.R.J. and Ryan, P. G. 2005. Roberts – Birds of Southern Africa. The Trustees of the John Voelcker Bird Book Fund.
- Keijl, G.O., Brenninkmeijer, A., Schepers, F. J., Stienen, E.W.M., Veen, J. and Ndiaye, A. 2001. Breeding gulls and terns in Senegal in 1998, and proposals for new population estimates of gulls and terns in north-west Africa. *Atlantic Seabirds* 3: 59–74.
- Lebreton, J.-D., Burnham, K.P., Clobert, J. and Anderson, D.R. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol. Monogr.* 62: 67–118.
- Parmelee, D.F., Fraser, W.R. and Neilson, D.R. 1977. Birds of the Palmer Station area. *Antarc. J. United States* 12: 14–21.
- R Development Core Team. 2003. R: A language and environment for statistical computing. R Foundation for Statistical Computing.
- Randall, R.M., Randall, B.M., Batchelor, A.L. and Ross, G.J.B. 1981. The status of seabirds associated with islands in Algoa Bay,

- South Africa, 1973–1981. *Cormorant* 9: 85–104.
- Ringsby, T.H., Sæther, B.E., Altwegg, R. and Solberg, E.J. 1999. Temporal and spatial variation in survival rates of a house sparrow, *Passer domesticus*, metapopulation. *Oikos* 85: 419–425.
- Ringsby, T.H., Sæther, B.-E., Tufto, J., Jensen, H. and Solberg, E.J. 2002. Asynchronous spatiotemporal demography of a house sparrow metapopulation in a correlated environment. *Ecology* 83: 561–569.
- Sæther, B.-E., Ringsby, T.H., Bakke, Ø. and Solberg, E.J. 1999. Spatial and temporal variation in demography of a house sparrow metapopulation. *J. Anim. Ecol.* 68: 628–637.
- Steele, W.K. 1992. Diet of Hartlaub's Gull *Larus hartlaubii* and the Kelp Gull *L. dominicanus* in the southwestern Cape province, South Africa. *Ostrich* 63: 68–82.
- Steele, W.K. and Hockey, P.A.R. 1990. Population size, distribution and dispersal of Kelp Gulls in the southwestern Cape, South Africa. *Ostrich* 61: 97–106.
- Underhill, L.G., Tree, A.J., Oschadleus, H.D. and Parker, V. 1999. Review of ring recoveries of waterbirds in southern Africa. Avian Demography Unit, University of Cape Town.
- Venables, W.N. and Ripley, B.D. 2002. Modern applied statistics with S. Springer-Verlag.
- Wanless, S., Harris, M.P., Calladine, J. and Rothery, P. 1996. Modelling responses of herring gull and lesser black-backed gull populations to reduction of reproductive output: Implications for control measures. *J. Appl. Ecol.* 33: 1420–1432.
- White, G.C. 2002. Discussion comments on: the use of auxiliary variables in capture–recapture modelling. An overview. *J. Appl. Stat.* 29: 103–106.
- White, G.C. and Burnham, K.P. 1999. Program MARK: Survival estimation from populations of marked animals. *Bird Study* 46: S120–139.
- Whittington, P.A., Martin, A.P. and Klages, N.T.W. 2006. Status, distribution and conservation implications of the Kelp Gull (*Larus dominicanus vetula*) within the Eastern Cape region of South Africa. *Emu* 106: 127–139.
- Williams, A.J., Cooper, J. and Hockey, P.A.R. 1984. Aspects of the breeding biology of the Kelp Gull at Marion Island and in South Africa. *Ostrich* 55: 147–157.
- Yorio, P. and Garcia Borboroglu, P. 2002. Breeding biology of Kelp Gulls (*Larus dominicanus*) at Golfo San Jorge, Patagonia, Argentina. *Emu* 102: 257–263.