Influence of food availability on demography and local population dynamics in a long-lived seabird

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Few studies have addressed the effects of food availability as a proximate factor affecting local adult survival in long-lived organisms and their consequences at local population dynamics. We used capture–recapture analysis of resightings of 10 birth cohorts of ringed Audouin's gulls, *Larus audouinii*, to estimate adult survival and dispersal (both emigration and immigration). For the first time, permanent emigration (the transient effect in capture–recapture analysis) was modelled for the whole population and not only for the newly marked birds. Gulls exploit to a large extent fishes discarded from trawlers, and a trawling moratorium established since 1991 has decreased food supply for the colony. This was used as a natural experiment of food availability to assess its effects on adult survival and emigration. These and other demographic parameters were used in a projection modelling to assess the probabilities of extinction of the colony under two scenarios of lower and higher food availability. Food availability (together with the age of individuals) influenced emigration probabilities, but not adult survival, which was estimated at 0.91 (s.e. = 0.02). When food was in shorter supply during the chick-rearing period, emigration was very high (*ca.* 65%) for younger breeders, although this rate decreased sharply with age. Probabilities of extinction were very high when food availability was low, and when environmental stochasticity was introduced, and only stochastic immigration from the outside seemed to prevent extinction. The results highlight the importance of dispersal processes in the population dynamics of long-lived organisms.

Keywords: Audouin's gull; *Larus audouinii*; dispersal; survival; food availability

1. INTRODUCTION

Population size is a state variable of central interest in many domains of ecology. Detailed demographic studies are required to address the processes underlying temporal variation in numbers (Yoccoz *et al.* 1998). This change is a function of births, deaths, immigration and emigration (i.e. fitness components or demographic parameters). Prospective perturbation analyses in long-lived species indicate that adult survival has the greatest potential impact on projected growth rate (e.g. Cairns 1992; Stearns 1992; Russell 1999; Saether & Bakke 2000; Cooch *et al.* 2001). One may thus expect that environmental factors have a greater influence on fitness components such as juvenile survival, recruitment or reproduction, than on adult survival (Lebreton & Clobert 1991). Several environmental factors such as food availability may influence the population dynamics of long-lived organisms, and as such, of seabirds (e.g. Cairns 1992; Furness 2003). It has been suggested that an increased food supply resulting from human activities (e.g. industrial fisheries, refuse dumps) is responsible for the substantial increase in numbers in populations of several opportunistic seabird species in recent decades (e.g. Croxall & Rothery 1991; Garthe *et al.* 1996). Most of the studies, however, have attributed this trend to the increase of fecundity and not of adult

survival or dispersal. Similarly, fisheries have also been suspected to threaten seabird populations because humans and birds compete for the same resource (e.g. fishes and squid). Stock overexploitation may have a negative influence on seabird population dynamics in this situation (Oro 1999; Tasker *et al.* 2000; Furness 2002), although there is also a lack of empirical data for that scenario.

To understand the process underlying the influence of food availability on variation in numbers in seabird populations, the demographic parameters covarying with resource availability have to be identified. Food availability influences different components of fecundity, such as laying dates (e.g. Safina *et al.* 1988; Oro *et al.* 1996*a*); clutch size (e.g. Oro *et al.* 1996*b*); egg size (e.g. Hiom *et al.* 1991; Bolton *et al.* 1992; Oro 1996; Ratcliffe *et al.* 1998) or breeding success (e.g. Springer *et al.* 1986; Monaghan *et al.* 1992; Phillips *et al.* 1996; Gill 1999). Nevertheless, there is little evidence of an influence of food availability on demographic parameters other than reproductive rates. Some studies have shown that there is a relationship between resource availability and deferred breeding (e.g. Monaghan *et al.* 1992; Wernham & Bryant 1998), adult survival (Pons & Migot 1995; Harris *et al.* 1997; Oro *et al.* 1999; Oro & Furness 2002) or local recruitment rates (Boekelheide & Ainley 1989; Oro & Pradel 2000). Most survival studies have been conducted at a single site, or a subset of locations and have addressed *local* survival (i.e. (1 − true mortality) × fidelity; Nichols *et al.* 1992; Brownie *et al.* 1993; Spendelow *et al.* 1995, 2002; Joe &

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Pollock 2002). Observed variation in local survival in wild animal populations may reflect variation in fidelity (i.e. variation in the rate of permanent emigration out of the study area). It is not clear whether previous results concerning the influence of environmental factors on 'adult survival' reflect genuine effects of adult mortality, or the confounding influence of permanent emigration. Yet, it has been shown that breeding failure is associated with increased breeding dispersal probability (e.g. Danchin *et al.* 1998; Oro *et al.* 1999). The influence of food availability on local survival may reflect the indirect influence of breeding failure on emigration probability (e.g. Boulinier *et al.* 1997).

Unequivocal evidence that food availability influences population growth in seabird populations is rare (Croxall & Rothery 1991), even though long-term datasets on both fish stock and seabird demographic parameters are becoming more available (Chapdelaine & Rail 1997; Harris *et al.* 1997; Crawford 1999; Oro & Furness 2002). Simulations of population dynamics under different scenarios of food availability have rarely been used to assess the possible effect of human activities such as fisheries and discarding on seabird populations, or they were based on sets of parameters that were not estimated using empirical data (MacCall 1984; Cairns 1992). We addressed the influence of discards from fisheries (i.e. an additional foraging resource) on the demographic parameters in a local population of Audouin's gulls (*Larus audouinii*), an endemic species breeding in the Mediterranean, and considered as vulnerable. We used an approach permitting distinction between adult survival and the probability of emigrating permanently out of the study area. We also used simulations to assess the viability of a local population and to estimate its extinction risk, considering several scenarios with variable food availability.

2. MATERIAL AND METHODS

(a) *Study area and the trawling moratorium*

Data were collected from 1974 to 2001 in a colony located on the Columbretes Islands (western Mediterranean: 39°51′ N 0°40′ E; figure 1). The study area is a volcanic outcrop (comprising three major islet groups) of 19 ha, located close to the edge of the continental shelf, 60 km off the mainland coast. Breeding numbers fluctuated greatly during the study. The site was colonized in 1974 (40 pairs) and breeding numbers reached 625 pairs in 1995. Only yellow-legged gulls (*Larus cachinnans*) regularly prey upon Audouin's gulls, especially on eggs and chicks (Martínez-Abraín *et al.* 2003).

A trawling moratorium was established from 1991 onwards to allow fish populations to recover from overfishing (Lostado *et al.* 1999). The moratorium concerned an area extending 220 km along the coast out to the limit of the continental shelf (see Oro *et al.* 1996*b* for more details). The moratorium was effective for two months every year, and it always overlapped one of the following stages of the breeding season: the laying stage (April–May), the incubation period and first weeks of the chick-rearing stage (May–June) or the chick-rearing stage (June–July). Discard availability was estimated using statistics of fish catches from fishermen's guild bulletins, which in this area are highly correlated with the amount of fish discarded (Oro & Ruiz 1997; Oro & Pradel 1999).
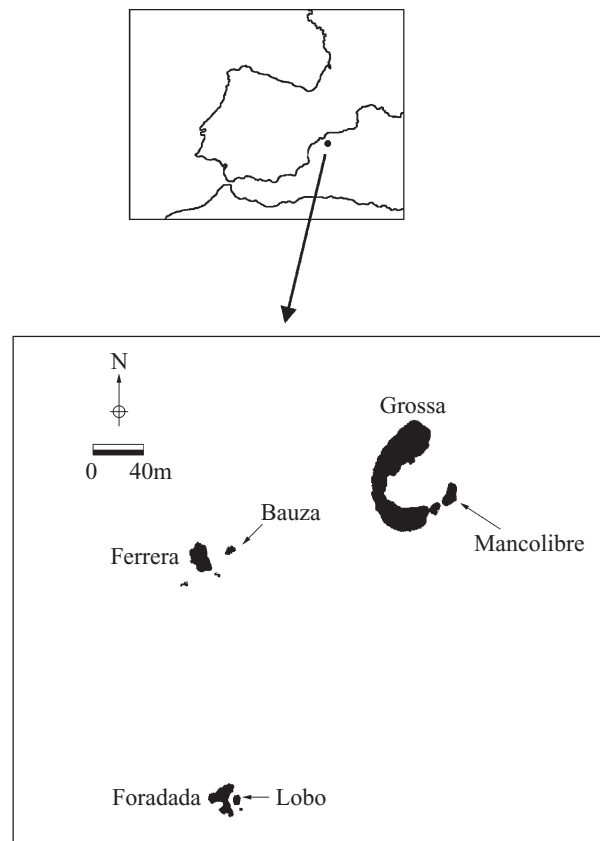
Figure 1. Map of the western Mediterranean (Iberian Peninsula) and the study area at Columbretes Islands.

(b) *Data collection*

Individuals were marked as fledglings from 1988 onwards using a plastic ring with a unique code (Oro & Pradel 2000). From 1988 to 1996, 843 chicks were ringed at the colony (range of 0–208 per year, depending on chick productivity). Complete breeding failure occurred in 1993 and 1997. From 1992 to 2000 (except for 1994) marked gulls were resighted from a distance using a telescope during the breeding season (from March to July). The total number of resightings was 1334. Only one resighting per individual and breeding season was retained for analysis. We also excluded immature birds (less than 3 years old, the youngest age of first breeding reproduction estimated in Audouin's gull; see Oro & Pradel (1999)). We assumed that all observed adult birds were breeders. We realize that this assumption may have consequences for our results, as we may have retained individuals breeding in other locations, and therefore having lower local survival. We eliminated resightings from birds also observed the same year in the neighbouring colony of the Ebro Delta and the Balearic Archipelago to minimize this possible bias. This was the best possible approach available as, for practical reasons, it is not possible to assess individual breeding status for every bird resighted in colonies. A total of 214 individuals were taken into account for analysis.

The number of breeding pairs was estimated in every year of the study except 1980 and 1981. Population size was assessed using nest counts, a standard procedure for the species (see Oro & Ruxton 2001). This approach provides moderately reliable estimates of population size, especially in such a small colony.

(c) *Adult survival and emigration out of the study area*

Adult survival was estimated from mark–recapture data (Lebreton *et al.* 1992). Many standard capture–recapture models rely on the assumption that all marked individuals have the same survival probability (e.g. Burnham *et al.* 1987; reviewed in Williams *et al.* 2002). Several sources of heterogeneity in survival probability among individuals lead to violations of the assumptions underlying capture–recapture models, one of which is the presence of transients. Transients (as opposed to residents) are individuals that leave the study area after first capture and thus have a local survival probability equal to zero (Pradel *et al.* 1997). The presence of transients in the marked sample may bias estimation of survival. Comparisons between models including a residency parameter $(1 - \tau) < 1$ (not all the individuals in the sample are residents) or equal to 1 (the marked sample includes residents only) addresses the presence of transients in the study population (Hines 1996). Importantly, the presence of transients indicates emigration out of the study area. This parameter cannot be used to assess the importance of emigration *sensu stricto* because it is assessed relative to the local survival probability of individuals recaptured several times (i.e. 'residents'; equation (2.1)). However, we cannot tell to what extent the local survival probability of individuals resighted several times reflects true survival (i.e. it may also incorporate permanent emigration out of the study area). The residency parameter assesses a 'relative' probability of dispersing in newly marked birds compared with birds with a longer history in the marked sample. Nevertheless, the influence of environmental factors such as food availability on the residency parameter provides insight into the relationship between these factors and the probability of emigrating permanently out of the study area.

We began with the Cormack–Jolly–Seber (CJS) model (ϕ_t, p_t), where ϕ is the local survival and p is the recapture (or resighting) probability (e.g. Pollock *et al.* 1990; Lebreton *et al.* 1992). This model had time-specific parameters. For model selection and assessment of the biological hypotheses guiding model development (Burnham & Anderson 1998), it is critical that the general model fits the data (Lebreton *et al.* 1992). Consequently, we first assessed the fit of the general model using the program U-CARE (Choquet *et al.* 2000). The program provides an insight into possible violations of the assumptions underlying the CJS model (see Burnham *et al.* 1987; Pradel *et al.* 1997). The components of several tests (e.g. TEST2 and TEST3) address the effect of first capture on future capture probability (e.g. trap-dependence: individuals may tend to avoid capture after being captured once) or survival probability.

The goodness of fit test showed that the CJS model (ϕ_t, p_t) did not fit our data (TEST2 + TEST3: $\chi^2_{18} = 33.44$, $p = 0.015$). All the deviations from expected values lay in TEST3.SR ($\chi^2_6 = 20.14$, $p = 0.003$). This indicates the presence of transient (or emigrating) individuals in the sample of individuals resighted in the colony for the first time. Other possible interpretations would be differences in survival (unexplained heterogeneity or increase in survival with age) or heterogeneity in dispersal propensity. Based on a previous study of survival in Audouin's gulls (Oro *et al.* 1999) we can rule out differences in survival as the cause of the significance of TEST3.SR. Indeed, the level of survival in this species is so high for all the age classes considered in our study (greater than 0.90) that it cannot explain the disappearance of many newly marked animals (young or otherwise). Differences in dispersal propensity as opposed to the presence of transients would result in the continued excess disappearance

of individuals seen only once previously in contrast to the disappearance of individuals seen at least twice previously. This was tested by recalculating TEST3.SR after discarding the first observation of every individual (Pradel *et al.* 1997). Then, TEST3.SR was no longer significant ($\chi^2_5 = 7.53$, $p = 0.184$) indicating that there was no remaining heterogeneity. We checked that the lack of significance could not be due to a loss of power by calculating TEST3.SR on the whole dataset but without the first and then without the last year, thus achieving similar sample sizes as when dropping the first observations. TEST3.SR was significant in two cases ($\chi^2_5 = 24.65$, $p = 0.0002$ and $\chi^2_5 = 18.37$, $p = 0.0025$, respectively). When TEST3.SR was ignored, the overall test did not indicate lack of fit (GOF test: $\chi^2_{12} = 13.20$, $p > 0.50$). Consequently, we developed models accounting for the presence of transients in the marked sample (Pradel *et al.* 1997). In these models, the probability $\tau(t)$ that an *unmarked* animal captured at time t is a transient is estimated in a two-age-class model as

$$\tau(t) = 1 - \phi^*(t)/\phi(t), \tag{2.1}$$

where $\phi^*(t)$ is the apparent survival rate of individuals newly observed in the colony, and $\phi(t)$ the survival probability of individuals resighted several times in the colony (in different years) (Pradel *et al.* 1997). However, this quantity, being relative to the number of *unmarked* animals captured at each occasion, will vary with the proportion of marked animals in the population, even if the intensity of transience remains constant. The biologically meaningful quantity is the proportion of transients relative to the whole population (even though transients can only be unmarked animals). To estimate this quantity (denoted T_t) in place of τ_t, we modified the data as when handling trap dependence (Pradel 1993). Capture–recapture histories were accordingly modified and the first survival $\tilde{\phi}$ in the two-age-class model, estimated separately from ϕ, now applied to all animals captured at a given occasion (not to the sole newly marked as ϕ^*); $\tilde{\phi}$ allowed us to estimate T_t as

$$\tilde{\phi}/\phi = 1 - T_i. \tag{2.2}$$

Working within a log–linear framework, we were then able to substitute $\log(1 - T_t)$ for any linear combination of covariates

$$\log(1 - T_t) = \log(\tilde{\phi}) - \log(\phi). \tag{2.3}$$

Several models with a transient effect (denoted $(T., \phi., p.)$; see notation in Pradel *et al.* 1997) were considered, always using the log-link function. We assessed several *a priori* ecological hypotheses based on factors that, in our view, could affect transience, survival or capture probabilities (table 1). We investigated the influence of discard availability on survival probability and the transient parameter. Hypotheses concerning food availability were assessed using ultrastructural models (e.g. Lebreton *et al.* 1992; Nichols & Kendall 1995) based on equation (2.3). Data on the amount of fish landed (i.e. as an index of food availability in the study area; see Oro *et al.* (1999)) each month were available for every year. We addressed whether food supply influenced transient or survival probability in four different ways, depending on the timing of the moratorium: (i) number of discards during the whole breeding season (March–July) (denoted by ε); (ii) number of discards only during the egg-laying and incubation periods (March–May) ($\varepsilon1$); (iii) number of discards only during the chick-rearing period (June–July) ($\varepsilon2$); (iv) whether the trawling moratorium occurred during the chick-rearing period (June–July) expressed as a categorical

Table 1. Summary of the different (T, ϕ, p) models built with SURGE to estimate the proportion of transients in the whole population (denoted T_t) and not only among the individuals newly observed, survival probability (ϕ), and recapture probability (p) depending on the biological hypotheses tested.

model notation	biological hypothesis
modelling T	
T	constant
T_a	2 age classes dependent: $\leqslant 4$ years (3 + 4 years) and older birds
T_A	depending on true age (from 3 to 12 years old)
T_ε	depending on availability of trawler discards during the whole breeding season (March–July)
$T_{\varepsilon 1}$	depending on availability of trawler discards during the laying period (March–April)
$T_{\varepsilon 2}$	depending on availability of trawler discards during the chick-rearing period (June–July)
$T_{\varepsilon 3}$	depending on availability of trawler discards during the chick-rearing period (June–July) as categorical (moratorium–not moratorium)
modelling ϕ	
ϕ_t	survival varied with time (years)
ϕ	constant survival
ϕ_ε	survival is dependent on availability of trawler discards for the whole breeding season
$\phi_{\varepsilon 1}$	survival varied with the availability of trawler discards during the laying period (March–April)
$\phi_{\varepsilon 2}$	depending on availability of trawler discards during the chick-rearing period (June–July)
$\phi_{\varepsilon 3}$	depending on availability of trawler discards during the chick-rearing period (June–July) as categorical (moratorium–not moratorium)
modelling p	
p_t	recapture is time dependent
p_A	recapture varied with true age (from 3 to 12 years old)
p	recapture is constant
p_e	recapture is dependent on effort of resightings (number of days sampled each year)

variable (denoted by $\varepsilon 3$) (see table 4 in electronic Appendix A, available on The Royal Society's Publications Web site).

Models also included year and age (from 3- to 12-year-old birds). Concerning age, two age classes were considered to achieve a reasonable sample size in each category: animals resighted for the first time at 3 or 4 years old (named younger birds) and older individuals (named older birds). Concerning recapture probability, we also developed models where p varies with resighting effort, measured as the number of days spent each year at the colony. We systematically assessed linear, quadratic or logarithmic (log) effects of age on transient, survival and recapture rates. Linear trends with age were denoted by A, the quadratic effects by A^2 and the log effects by $\tilde{A}$. Some models were successively fitted keeping transient probability constant beyond a given age (i.e. a plateau for different ages), considering that older birds are more likely to have bred earlier and that breeding experience may influence this parameter (see Oro *et al.* 1999; Oro & Pradel 2000). For instance, $(T_{\tilde{A}5}, \phi, p_t)$ designated a model with a log trend in transient probability up to age 5 years, with constant survival, and with time-specific recapture probability. We also considered food availability and its effects on survival, and we used the same functions (linear, quadratic or logarithmic) accounting for possible relationships between them.

Analyses were performed using software program SURGE 4.2 (Cooch *et al.* 1996). Model notation followed Lebreton *et al.* (1992). A model including two factors and their interaction was described using an asterisk. Additive models were described using a '+' symbol instead. For instance, $(T_{a*t}, \phi_{a*t}, p_{a*t})$ designated a model where transient, survival and recapture probabilities varied with age and time, with the effect of time potentially different in different age classes. The biological hypotheses underlying the structure of models were assessed using AIC (Akaike Information Criterion). Models with the lowest values of AIC were retained as good candidate models (Lebreton *et al.* 1992; Anderson & Burnham 1999*a*,*b*; Reboulet

et al. 1999). Models with differences in AIC values lower than 2 were considered as 'equivalent' (i.e. data were insufficient to lead to definitive conclusions concerning the process that gave rise to the data; Burnham & Anderson (1998)). Comparisons among models using information criteria allow us to assess the hypotheses in question, even when the corresponding models have a different structure, which precludes the use of test statistics such as likelihood-ratio tests (Burnham & Anderson 1998).

(d) *Extinction probability*

Extinction probability was estimated using a matrix population model accounting for demographic and environmental stochasticity (e.g. Caswell 2001). We considered demographic stochasticity because the small size of our study population in some years made it likely to be subject to that type of process (e.g. Caswell 2001). Environmental stochasticity was considered to account for the variation in environmental factors other than food availability (e.g. climate). Environmental stochasticity takes into account the temporal variability in demographic estimates. We used a Monte Carlo approach and simulated population numbers over time using different sets of parameters and sources of uncertainty (see table 2; e.g. Caswell 2001). Model development was based on vital rates mainly estimated at the Columbretes colony: adult survival and emigration (this study), and fecundity (from literature). Other vital rates such as immature survival, age at first breeding and proportion of breeders arise from studies carried out at a neighbouring colony located at the Ebro Delta (Oro 1998; Oro *et al.* 1999; Oro & Pradel 2000). Since some first-time breeders (especially 3- and 4-year-old birds; see § 3) from the Delta colony emigrated to other colonies (Oro *et al.* 1999), we also took immigration into account (see § 2e). We assumed a balanced sex ratio (Genovart *et al.* 2003). All parameters were drawn from uniform probability distributions (see below).

Table 2. Demographic parameters used in the Monte Carlo simulations depending on availability of food around the colony during the breeding season.
(Only mean values are shown.)

| | estimate | | |
parameter	higher food availability	lower food availability	references
juvenile survival 1 year	0.79		Oro (1998)
immature survival 2 years	0.88		Oro (1998)
adult survival	0.91		this study
proportion of emigrants[a]	0.50–0.21	0.63–0.40	this study
proportion of breeders[b]	0.84–0.90		Oro & Pradel (2000)
fecundity[c]	0.15–0.41–0.33–0.11	0.92–0.07–0.01–0.00	Oro *et al.* (1996*b*); own data

[a] Only younger breeders (3–4-year-old birds) are considered.
[b] Only 3- and 4-year-old birds are considered since proportion of breeders of birds older than 4 years is 1 (from Oro & Pradel 2000).
[c] Empirically derived probability distribution of each female producing 0, 1, 2 or 3 fledglings.

We considered two different scenarios: (i) the first scenario corresponds to a situation where trawlers operate normally around the colony during the breeding season (i.e. situation with higher food availability); (ii) the second scenario corresponds to a situation where the trawling moratorium overlaps with the chick-rearing period (i.e. situation with lower food supply). The only two parameters assumed to be affected by food were the proportion of emigrants (higher when food availability was lower; see § 3) and fecundity (positively associated with food availability; e.g. Oro *et al.* (1996*a*, 1999)). We only included a probability to emigrate for younger breeders (3–4-year-old birds) to reduce complexity of the matrix, because this parameter sharply decreased at older ages (see § 3). We know that adult survival was not affected by food availability (see § 3) and assumed that immature survival and proportion of breeders were not affected either. We started simulations using numbers corresponding to 1991, when the trawling moratorium was first established and 225 females bred (Oro 1998). We also considered the number of females breeding in the 3 years before (i.e. 1998–1990) to take into account their offspring produced during that period of time and that started recruiting into the breeding segment of the population in 1991. Models include several sources of stochasticity. Consequently, different runs for the same parameter values can lead to different results. We therefore simulated 500 trajectories over a 100-year time interval. Input parameters were randomly selected from uniform distribution between the upper and the lower 95% confidence limits for each parameter. However, some of this variability can arise from sampling (measurement) variation and this could overestimate this stochasticity and its effects on extinction probabilities (Burnham & White 2002). We used the proportion of extinct trajectories (when population size n at time t is 0) to estimate the extinction probability at time t_i. For each scenario, we ran one set of simulations with demographic stochasticity, and one set with both demographic and environmental stochasticity. Simulations were visually compared with the observed trajectory of local population size during the period 1991–2001 (for which data on breeding numbers were available). Formal comparisons would be difficult because we did not only consider the mean trajectory, but also variability (Brook *et al.* 1997).

(e) *Immigration from the Ebro Delta colony*

We estimated the proportion of immigrants from the nearest colony (the Ebro Delta), where chicks have also been marked

since 1988 (6523 chicks up to 1997). The number of individuals born in the Ebro Delta observed at the Columbretes Islands was 464 over the study period (1992–2000). The expected number N_i^t available to breed at the Columbretes Islands in year t (from 1992 to 2000) from the pool marked in year i at the Ebro Delta (from 1988 to 1997) is

$$N_i^t = N_i \cdot \phi_j \phi^{t-i-3} \cdot b_{t-i},$$

where N_i is the number of individuals marked in year i, ϕ_j is the juvenile survival from birth to age 3 years (age of first breeding), ϕ is the adult survival probability and b_{t-i} is the breeding propensity, i.e. the proportion of breeders among the survivors, at age $t - i$.

Let n_i^t be the number of individuals born in year i and resighted in year t. The ratio n_i^t/N_i^t estimates the probability of presence at the Columbretes colony times the probability of detecting a bird breeding in that location. We assume that the demographic parameters and detection probability do not depend on the origin of the birds (from the Columbretes Islands 'C' or from the Ebro Delta 'E'), nor on the year of ringing. Then relative presence (rp) of birds from the Ebro Delta colony at the Columbretes Islands can be estimated as follows: $(n_{iE}^t/N_{iE}^t)/(n_{iC}^t/N_{iC}^t)$. Finally, if we assume that this quantity does not depend on i, the year the individual was marked, but only on t, the year the individual was resighted, then relative presence can be estimated using the following formula:

$$\mathrm{rp}_t = \sum_i (n_{iE}^t/N_{iE}) \bigg/ \sum_i (n_{iC}^t/N_{iC}).$$

An estimate of the variance of rp_t is obtained by the delta method as

$$\frac{\left\{\sum_i \dfrac{n_i^t(N_i - n_i^t)}{(N_i)^3}\right\}_E}{\left\{\left(\sum_i \dfrac{n_i^t}{N_i}\right)^2\right\}_C} + (\mathrm{rp}_t)^2 \frac{\left\{\sum_i \dfrac{n_i^t(N_i - n_i^t)}{(N_i)^3}\right\}_C}{\left\{\left(\sum_i \dfrac{n_i^t}{N_i}\right)^2\right\}_C}.$$

Finally, 95% confidence intervals (CI) were calculated to assess whether there were significant differences between the different values of rp_t (see also Oro & Pradel 2000).

3. RESULTS

The first set of models assessed (table 5 in electronic Appendix A) led to a candidate model ($T_{\bar{A}}$, ϕ, p_t), where
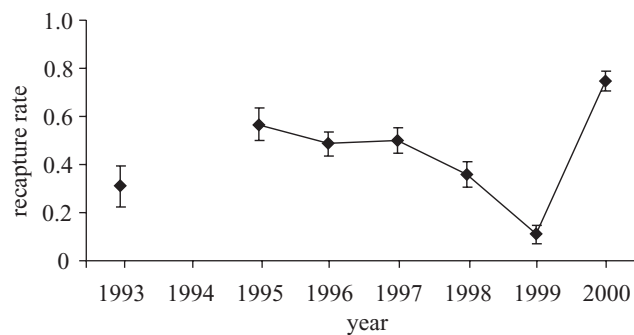
Figure 2. Recapture probabilities for Audouin's gulls at the Columbretes Islands during the study period (1992–2000), under the finally selected model (see § 3). Bars show standard errors. There were no recaptures in 1994.
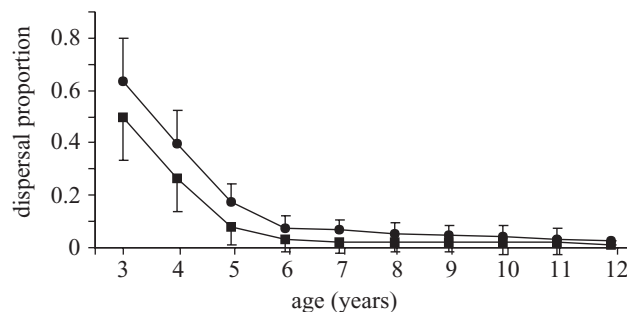

Figure 3. Proportion of transients depending on the age of individuals and food availability: filled circles represent a year with trawling moratorium overlapping with the chick-rearing stage; filled squares show a year with normal trawling activity, i.e. a year with higher food availability. Bars show standard errors.
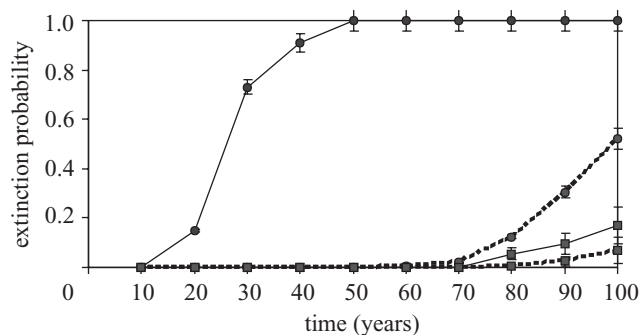

Figure 4. Probability of extinction (and standard errors) estimated through Monte Carlo simulations of the two different scenarios considered: when trawling moratorium coincided with the chick-rearing stage (lower food availability), shown by filled circles, and when trawler discards were normally available (higher food availability), shown by filled squares. Solid lines show the simulations with demographic and environmental stochasticity and dashed lines show the simulations with only demographic stochasticity.

survival of resident birds did not vary with time, whereas residency probability varies with log(age). Models with recapture varying with time had lower AIC values than models with constant recapture or with an effect of resighting effort. We also addressed the hypothesis that emigration of newly marked birds was progressive and also influenced second resighting year (model denoted as (T_ω, ϕ, p_t)). We found no evidence of such an effect (table 6 in electronic Appendix A).

In the next step, we considered models including an influence of discard availability both on survival, transient and recapture probabilities. The effect of food availability on recapture probability could reflect the attendance of individuals to the nest and the probability of skipping reproduction for an experienced breeder. Most of the models had AIC values very close to that of the model selected in the previous step (table 6 in electronic Appendix A), but one model showed a significantly lower AIC value (denoted as $(T_{\tilde{A}+\varepsilon 3}, \phi, p_t)$). In this model transient probability varies with log(age) and food availability during the chick-rearing period, expressed as activity or moratorium of trawlers (table 6 in electronic Appendix A). This provides evidence that discard availability influences the probability of emigrating permanently out of the Columbretes Islands. We also built a set of models where food availability during different stages of the breeding cycle influences survival in resident birds or their recapture probability, but none of these models had lower AIC values than the previous one. Finally, we assessed an *a posteriori* hypothesis based on the provisionally selected model in the first step (table 5 in electronic Appendix A) and eliminated the influence of age on transient probability. The AIC of this model (table 6 in electronic Appendix A) was higher than that of the model including age. Estimated adult survival was 0.910 (95% CI: 0.887–0.931) and recapture probabilities ranged from 0.120 (95% CI: 0.104–0.129) to 0.746 (95% CI: 0.598–0.887) (see figure 2). There is a negative association of the probability of emigrating out of the Columbretes with both food availability and age (figure 3). There are two extreme situations (years), with the trawling moratorium overlapping with the chick-rearing period (lower food availability) or with normal trawling activity (higher food availability). When food availability was lower, the proportion of younger emigrants was high, *ca.* 65%. When food was readily available, this proportion was still high, but lower,

ca. 50%. In both cases the proportion of dispersing birds decreased sharply with age, and it was lower than 10% for 5-year-old and older birds (figure 3).

Monte Carlo simulations showed that extinction probability varied greatly with food availability during chick rearing. When demographic stochasticity was considered, extinction probability increased with time, especially when the trawling moratorium overlapped with the chick-rearing stage (figure 4). When environmental stochasticity was incorporated (table 3), the difference in trend between the two situations regarding food availability was similar, but overall extinction probability was higher (figure 4). Assuming that variance of the most sensible demographic parameter (adult survival) was estimated with high accuracy, we considered that the potential sampling error incorporated in environmental stochasticity was low. Under a scenario with lower food availability (trawling moratorium effective), all trajectories were extinct at time 100 (i.e. 100% probability of extinction), and mean extinction time was 26.9 years (s.e. = 0.8; figure 5*a*). When food availability was higher (i.e. when discards were available), extinction probability dropped to 20%, and mean extinction time increased to 61.4 years (s.e. = 2.2; figure 5*a*).

Table 3. Demographic parameters of Audouin's gull at the Columbretes Islands with environmental stochasticity.

parameter	mean	s.d.
juvenile survival 1 year	0.79	0.30
immature survival 2 years	0.88	0.25
adult survival	0.91	0.06
breeding dispersal 3 years	0.56	0.40
breeding dispersal 4 years	0.29	0.38
proportion of breeders 3 years	0.84	0.20
proportion of breeders 4 years	0.90	0.10
fecundity bad year[a]	0.11	0.30
fecundity good year[b]	1.10	0.20

[a] When trawling moratorium overlapped with the chick-rearing stage (in chicks per pair).
[b] When trawler discards were normally available (in chicks per pair).

Breeding numbers have fluctuated greatly from 75 to 625 pairs (figure 6) since the establishment of the trawling moratorium in 1991. When the two simulated trajectories were compared with observed population dynamics during these years (figure 5b), both scenarios led to projected numbers consistent with observed numbers in early and last years of the study period. However, for the period 1995–1997, the observed population size was substantially larger, even larger than simulated trajectories taking into account higher food availability from discards (figure 5b). This corresponds to the years with high emigration rates from the Ebro Delta due to a predatory event (Oro *et al.* 1999). In fact, we recorded a substantial increase of immigrants from the Ebro Delta in 1995 (figure 5c), which coincided with the increase in population size at the Columbretes colony. There was actually a positive correlation between the relative presence of females dispersing from the Ebro Delta to the Columbretes in a given year and the number of females breeding at the latter colony ($r = 0.76$, $n = 9$, $p = 0.017$).

4. DISCUSSION

Our results provided unambiguous evidence that food availability influences the demography of a seabird local population. Importantly, we found that food availability influences the probability of emigrating permanently out of the study area, but not survival. The sensitivity of population growth rate to emigration has seldom been thoroughly addressed, and populations have often been explicitly or implicitly considered as 'isolated' in empirical studies. Indeed, *local* survival is often interpreted as *true* survival, and emigration ignored or considered as negligible (see Boulinier *et al.* 1997 for a discussion of this topic). Yet, emigration of breeders corresponds to loss of individuals in the critical stage with regard to population growth in long-lived species (e.g. Saether & Bakke 2000), and is approximately equivalent to mortality in local populations. Dispersal (both immigration and emigration) is thus one of the main demographic processes governing changes in numbers. Despite the remarkable number of models of dispersal evolution (Johnson & Gaines 1990), MacDonald & Johnson (2001) emphasized that 'there remains an almost complete absence of empirical data on
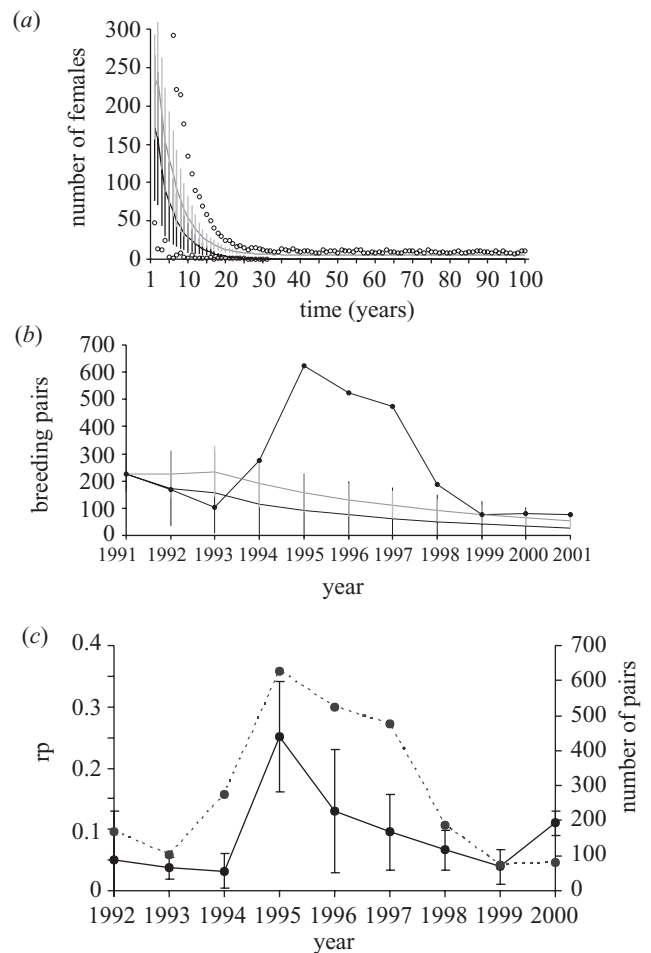

Figure 5. (a) Number of female breeders at Columbretes Islands from the Monte Carlo simulated trajectories after a 100-year interval and taking into account demographic and environmental stochasticity. The two scenarios considered are: with lower food availability (when trawling moratorium was established; solid line) and with higher food availability (when trawlers discards were available; dashed line). Lines show the mean trajectory over the different runs, bars show the standard error and circles show the lowest (of the lower food scenario) and highest (of the higher food scenario) values of the different trajectories at each time interval. (b) Population size estimates at the colony since the establishment of the trawling moratorium (solid line and circles) and simulated trajectories for the same period of time under the two scenarios (same legends). (c) Immigration of Audouin's gulls born in the Ebro Delta to the Columbretes Islands during 1992–2000 expressed as a relative presence (rp, see § 2) probability (± 95% CI); a dashed line shows the population size estimates at the colony throughout this period (see text).

dispersal and other relevant behavioural parameters in recent population extinction studies'. The probability of emigrating increased when food availability decreased during the chick-rearing period. It can be proposed that this type of dispersal strategy is consistent with what has been identified as 'conditional' dispersal (i.e. phenotypic plasticity in dispersal probability; Ims & Hjermann (2001); Ronce *et al.* (2001)). Although some other factors can also be involved in emigration, there is extensive evidence that breeding failure can have an important influence (e.g. Danchin *et al.* 1998; Doligez *et al.* 1999; Oro *et al.* 1999).
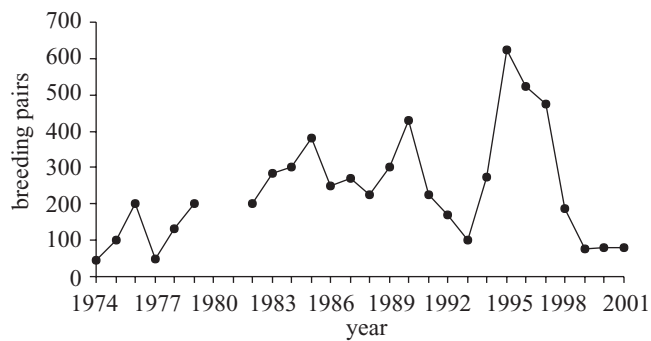
Figure 6. Annual population size (as number of breeding pairs) of Audouin's gulls at the Columbretes Islands. Estimates are from the colonization of the site until 2001, except for the period 1980–1981.

Results showed that age also influenced emigration to other local populations (Oro & Pradel 1999). The decrease in the probability of emigrating with age was already found in other local populations of Audouin's gull (Oro *et al.* 1999) and may reflect a positive influence of age on breeding success (e.g. Curio 1983; Pärt & Forslund 1995). Identification of the cues that animals rely on to make dispersal decisions is important to understand selective pressures involved in the evolution of dispersal (Danchin *et al.* 2001; Greene & Stamps 2001; Ronce *et al.* 2001).

The dynamics of the Columbretes local population is influenced not only by dispersal to other sites (mediated by food supply), but also by immigration, mainly from the Ebro Delta. Without this immigration, the Columbretes population would have decreased faster than observed due only to the local environmental features (i.e. local food availability depending on trawling activity). Only when a catastrophic event occurred at the Ebro Delta did the demographic balance of emigrants between the two colonies clearly favour the Columbretes colony. However, dispersal probabilities from the Ebro Delta to the Columbretes are still unknown, and the potential influence of immigration from the former colony on the dynamics of the latter deserves further study. For instance, low dispersal probabilities from the Ebro Delta would imply large numbers of immigrants recruiting to the Columbretes, owing the size of the former colony. It has to be pointed out that we could not introduce a dispersal probability from the Ebro Delta in our population modelling, which could by itself prevent extinction of the Columbretes colony through a rescue effect of the demographic sink (e.g. Harding & McNamara 2002; Hill *et al.* 2002). Despite this partial lack of knowledge, our results suggest that dispersal and immigration processes are crucial in the dynamics of metapopulations and the extinction–colonization events (Hanski 1999), which have been rarely addressed in long-lived organisms (Oro & Ruxton 2001; Cooch *et al.* 2001; Hill *et al.* 2002). The growth rate of the Columbretes local population fluctuated greatly from year to year (up to 169% increase and 75% decrease; see figure 6) clearly showing a dramatic influence of these transfer processes, which can mask the influence of local demographic parameters. Emigration and immigration can occur every year in a local population and an observed stability does not imply an absence of these two processes

(Oro & Ruxton 2001). Source–sink dynamics are in a non-equilibrium stage, with the source (the Ebro Delta, with a density-independent environment; see Oro (1999)) also attracting recruits from the sink (the Columbretes; see Oro & Pradel (1999, 2000)). Extinction of the sink is only prevented by large stochastic effects typical of non-equilibrium environments (DeAngelis & Waterhouse 1987), such as large immigration from the Ebro Delta after a predatory event (see Dias 1996; Holt 1997). Environmental stochasticity actually played an important role in the probabilities of extinction of the Columbretes colony, as is usual when a large variance occurs in the rate of population growth (Lande 1993).

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