

Inferring dispersal dynamics from local population demographic modelling: the case of the slender-billed gull in France

A. Doxa^{1*}, A. Besnard¹, A. Bechet², C. Pin³, J.-D. Lebreton⁴ & N. Sadoul³

¹ Centre d'Ecologie Fonctionnelle et Evolutive (UMR 5175), Ecole Pratique des Hautes Etudes, Biogéographie et Ecologie des Vertébrés, campus CNRS, Montpellier Cedex 5, France

² Centre de Recherche de la Tour du Valat, Arles, France

³ Les Amis des Marais du Vigueirat, Arles, France

⁴ Centre d'Ecologie Fonctionnelle et Evolutive (UMR 5175), campus CNRS, Montpellier Cedex 5, France

Keywords

Larus genei; capture–recapture; survival; recruitment; Mediterranean Sea; dispersion; population growth rate.

Correspondence

Aggeliki Doxa, Centre d'Ecologie Fonctionnelle et Evolutive (UMR 5175), Ecole Pratique des Hautes Etudes, Biogéographie et Ecologie des Vertébrés, campus CNRS, 1919 route de Mende, 34 293 Montpellier Cedex 5, France
E-mail: aggeliki.doxa@gmail.com

Editor: Res Altwegg

Associate Editor: Michael Schaub

*Current address: Institut des Sciences de l'Evolution, UMR 5554, CNRS, Université Montpellier 2, CC065, Place Eugène Bataillon, 34095 Montpellier, Cedex 05, France

Received 26 September 2012; accepted 28 March 2013

doi:10.1111/acv.12048

Introduction

As discrete animal populations are often connected by emigration and immigration processes, a meta-population approach (Hanski & Gilpin, 1997) is typically necessary in order to assess the viability of threatened species and propose sound conservation measures (Oro & Ruxton, 2001; Reed *et al.*, 2002; Drechsler *et al.*, 2003; Crooks & Sanjayan, 2006; van Teeffelen, Cabeza & Moilanen, 2006; Radchuk, WallisDeVries & Schtickzelle, 2012). Despite the evidence for this, field managers and conservation agencies are generally constrained to work on the management of single populations of rare and endangered species. In addition, they are often restricted by territorial boundaries that

Abstract

Although it is today accepted that population viability analyses are needed at a meta-population level for most species, usually only single populations are monitored in the context of management and conservation programmes. This paper outlines a fairly general and easy-to-implement approach based on counts and capture–recapture data that allow the dynamics of single populations to be assessed even when they are highly connected to other populations. This approach was motivated by a study of the French population of the slender-billed gull *Larus genei*, which experienced a sharp population increase in the 1980s and 1990s, suggesting that the species was not at risk of extinction. However, several recently raised concerns indicate that the observed population increase is unlikely to have been achieved uniquely by an intrinsic growth rate. We estimated local adult survival probability at 0.81 (0.79–0.83), which is considerably lower than that of other gull species of comparable size. Moreover, local fecundity observed in slender-billed gulls [0.66 (0.47–0.85)] is lower than that observed in similar species. Massive reproduction failures and the low demographic parameters observed could be caused by chick exposure to aerial and terrestrial predation, leading to permanent emigration. Unrealistically high demographic parameter values would be needed to generate the observed local population increase. The results of our study indicate that connections with other neighbouring populations are responsible for the local population dynamics, and that about 10% of the individuals may be immigrants into this local population annually. However, our results suggest that the population of the slender-billed gull may be stable at the west Mediterranean scale. The high annual fluctuations of population size observed at a larger scale also highlight the necessity for coordinated international action to protect a maximum of potential breeding sites in order to protect the species.

do not take into account ecological processes. This limitation is particularly detrimental for species occupying areas of habitat spread over several countries [e.g. the greater flamingo (Balkız *et al.*, 2010)]. Such species require coordinated international plans, which are difficult to achieve in practice.

Yet to be effective, conservation plans for species with high dispersal abilities need to focus on demographic traits, including immigration and emigration processes between local subpopulations. This can help, for instance, to identify the relative roles of the different habitat areas in the global dynamic of the system (Gyllenberg & Hanski, 1997; Akçakaya, 2000; Cam *et al.*, 2004; Nicol *et al.*, 2010; Ross & Pollett, 2010) and can reveal the importance of the exchange

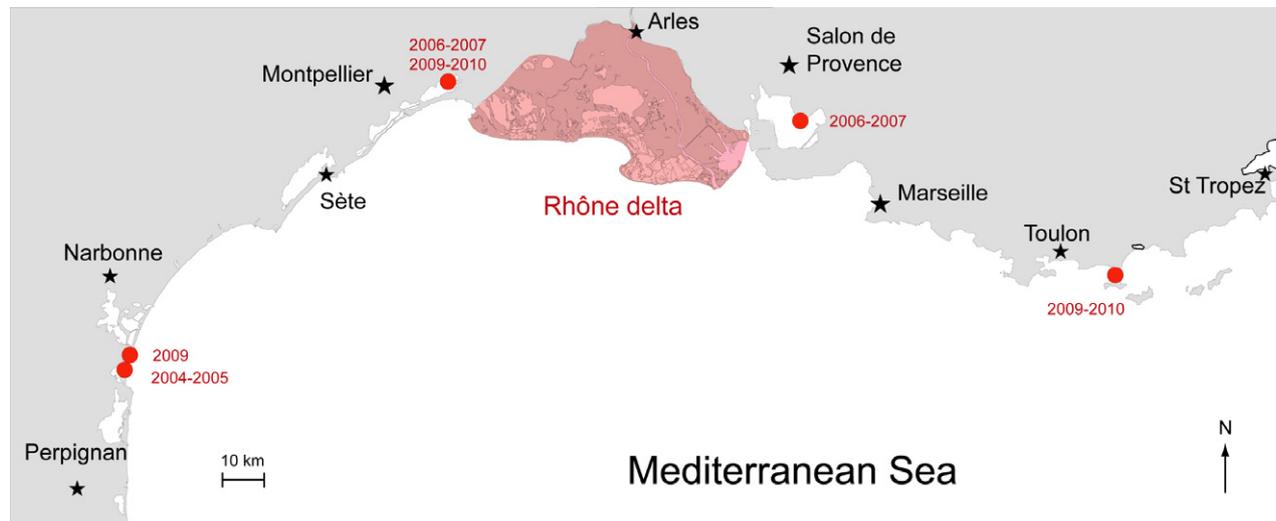


Figure 1 Breeding area (southern France) of the French slender-billed gull *Larus genei* population. The red zone is the Camargue (the Rhône delta), an area occupied every year since 1973. The red dots represent the breeding colonies outside the Camargue and the years they were used. The stars show the main towns in the area.

between subpopulations to their persistence (Crooks & Sanjayan, 2006; Kleinhans & Jonsson, 2011). Such demographic studies require the marking and monitoring of a large number of individuals simultaneously in several habitat areas. Although this is often possible at a local scale (see, e.g. Peron, Lebreton & Crochet, 2010b), it is rarely the case for species with a large range (but see Balkız *et al.*, 2010). Consequently, many conservation initiatives are developed based only on the knowledge of the local population dynamics and may sometimes be inappropriate.

This study was prompted by the intriguing dynamics of the French population of the slender-billed gull *Larus genei*. In France, only one or two pairs of slender-billed gulls were observed sporadically between 1951 and 1967. The first regular breeders were observed at the beginning of the 1970s, with 13 pairs reported in 1973. Over the following decade, the numbers stayed low, varying between 13 and 26 pairs until 1985 (Isenmann & Sadoul, 1999). In 1988, the number of breeding pairs reached 286, and then showed exponential growth until 1995 (Sadoul, 1996). Since then, numbers have stabilized and vary between 560 and 850 pairs, depending on the year. The sharp increase in numbers in the 1980s and 1990s suggested that this local population was not in particular danger of extinction. However, several authors have pointed out that such an increase is unlikely to have been achieved solely by an intrinsic growth rate in a species with such low fecundity (1–2 chicks), and may have been the result of a large-scale immigration (Sadoul, 1997; Sadoul, 1998; Isenmann & Sadoul, 1999). Moreover, as the breeding success is low, the French population may have acted as a sink flowed in by source populations.

The main questions our study sought to address were: does the French population’s current and past growth rate rely solely on an intrinsic dynamic? If not, can the importance of the emigration/immigration processes be quanti-

fied? To attempt to respond to these questions, our study involved three main steps: first, we estimated the demographic parameters of slender-billed gulls in the south of France using resightings of birds ringed from 1997 to 2009. Secondly, we used these estimates to parameterize matrix population models aimed at evaluating whether the observed growth rates matched those predicted by local demographic parameters. Lastly, we estimated the number of immigrants to the local population. We developed an approach that allows meta-population functioning to be inferred based on the local population dynamics, taking into account exchanges with other populations.

Material and methods

Field procedures

The number of breeding pairs of slender-billed gulls in France has been estimated since 1956 by nest counts at the peak of the laying period (Sadoul, 1996). All colonies are monitored and counted weekly, and the total number of breeders counted in each colony is noted. The peak of the laying period corresponds to the week with the highest number of breeders, also mentioned as peak of abundance. Before 2004, all colonies of the species in France were located in the Camargue (the Rhône delta). After this period, colonies began to appear in other areas along the French Mediterranean coast (Fig. 1). Although the species is rare, it is conspicuous, so we are confident that all French colonies were detected. All the colonies were monitored, and nest counts were organized every three years between 1973 and 1991, and annually since 1993. Based on weekly counts, regional breeding numbers were estimated each year at the peak of abundance.

At 4 and 8 days old, slender-billed gull chicks abandon the nest and form a crèche around the colony site (Isenmann, 1976). To monitor the birds, a few days before the chicks fledge, they are pushed into a corral, captured and ringed with a metal ring from the French National Museum of Natural History and a PVC ring engraved with a unique three-letter code that is readable using a telescope. A total of 3988 chicks, more than 90% of all slender-billed gull chicks born in France, were ringed between 1997 and 2010 (N. Sadoul, unpubl. data). Using mobile bird hides, subsequent observations of ringed birds have been conducted every year on all colonies, from the time of bird settlement to the last fledging, providing a total of 12 602 resightings of 900 adult and immature birds.

Because this species forms crèches with their young, breeding success (i.e. the number of fledglings per pair) is difficult or even impossible to estimate at an individual level. Consequently, we estimated the fecundity per colony (f hereafter), as the number of chicks in the crèche (before fledging) divided by the number of nests counted in the colony at the peak of laying. Before 1997, chicks in the crèche were counted from a distance a few days before the first fledging. Since 1997, almost all the chicks in each colony have been caught for ringing – resightings after ringing have allowed the percentage of non-caught chicks to be estimated.

Statistical analyses

Our method relies on local demographic parameter estimates and counts and requires only elementary knowledge of matrix population modelling (Caswell, 2001). This approach expands the method proposed in Peery, Becker, & Beissinger (2006) by permitting the direct estimation of the number of immigrants in the population.

Calculation of the population growth rate

The breeding population growth rate was estimated for the whole period of 1973–2010, as well as for two separate periods: (1) 1973–1997: a period of population expansion (see Fig. 2) and (2) 1997–2010: a period of apparent stabilization of breeding population size despite some fluctuations. Because counts were not performed annually during the first period, we used a regression procedure to estimate the average population growth rate according to Morris & Doak (2002). This regression procedure consists of estimating the mean of $\log(N_{i+1}/N_i)/\sqrt{t_{i+1}-t_i}$.

Model selection and demographic parameter estimations

Local demographic parameters (i.e. age-specific survival and recruitment probabilities) were estimated using resightings of ringed birds available from 1997 to 2010. A goodness-of-fit test conducted on all marked individuals but newborns using U-care (Choquet *et al.*, 2009a) indicated both transience and trap dependence (Test 3G.SR:

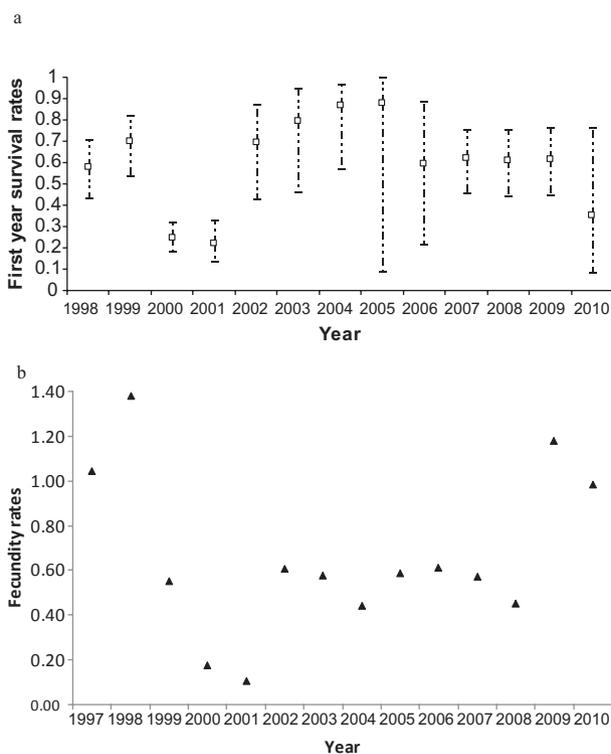


Figure 2 (a) First-year survival rates over time. Confidence intervals (95%) are shown in dashed lines. (b) Fecundity rates over time.

$\chi^2_{11} = 30.89$, $P = 0.001$ and Test 2.CT: $\chi^2_{10} = 53.33$, $P < 0.001$). The simultaneous detection of these effects generally results from heterogeneity in individual resighting probability (Pradel, 1993; Pradel *et al.*, 1997b), which can bias parameter estimates, especially survival probability (Pradel *et al.*, 1997a; Prévot-Julliard, Lebreton & Pradel, 1998). We thus used multi-event models that handle this type of heterogeneity and provide unbiased demographic parameter estimates (Pradel, 2005). Based on Peron *et al.* (2010a), we estimated the resighting probability of breeding slender-billed gulls in the colonies for two discrete heterogeneity classes (hc hereafter), that is, (1) breeders frequently seen and (2) breeders less frequently seen (coded as ‘B+’ and ‘B-’ hereafter). Four types of parameters were then estimated: (1) apparent survival probability (hereafter simply noted as ‘survival’ or ϕ); (2) probability of recruitment into the breeding population (r hereafter); (3) transition probability between heterogeneity classes of resightings (an individual may switch between classes over their lifetime) (tr hereafter); (4) resighting probability (p hereafter), which differs between the two classes of heterogeneity.

We considered time and age effects on survival, reproduction and recapture, whereas transition rates were set constant across heterogeneity classes. We considered two or three age classes in survival rates depending on the models as survival is known to vary with age in Larids (Navarro *et al.*, 2010). Access to reproduction is also known to be age-specific in long-lived birds (Clobert *et al.*,

1994; Pradel & Lebreton, 1999), so we considered two or three age classes for first recruitment probabilities. Because slender-billed gulls breed at extremely high densities (Cramp & Simmons, 1985; del Hoyo, Elliot & Argatal, 1996), the breeding status of an individual observed at the colony remains uncertain. Recruitment was thus modelled as the age-specific probability of access to a breeding site (i.e. of being observed within a colony) rather than age-specific breeding probability *per se*. As resighting probabilities often vary over time and are lower for first-year individuals, we considered a 2-age-class, time-dependent model, allowing for differences between the two heterogeneity classes (B+ and B-). The general model had thus the following structure (using the notation of Lebreton *et al.*, 1992): $\phi_{a_3^*t} r_{a_3^*t} U_c p_{a_2^*hc^*t}$.

Using a stepwise backward elimination of parameters, we progressively tested simpler models by first simplifying temporal effects on s , r and p and then decreasing the number of age classes considered where possible. Models were run using E-Surge (Choquet, Rouan & Pradel, 2009b). Matrices used are given in ESM-1. Model selection was based on the corrected Akaike information criterion (AICc). For AICc differences less than 2, models with fewer parameters were retained (Burnham & Anderson, 2002).

Retrospective analysis of population dynamics

We modelled the population dynamics of the slender-billed gull in France using a linear time-invariant-female-based matrix model:

$$N_{t+1} = A * N_t$$

where N_t is the vector of abundance of the age classes at time t and A is the population projection matrix corresponding to a post-breeding census (Lebreton & Clobert, 1991; Caswell, 2001):

$\phi_1 * \psi_1 * f * 0.5$	$\phi_2 * \psi_2 * f * 0.5$	$\phi_3 * \psi_2 * f * 0.5$	$\phi_2 * f * 0.5$	$\phi_3 * f * 0.5$
$\phi_1 * (1 - \psi_1)$	0	0	0	0
0	$\phi_2 * (1 - \psi_2)$	$\phi_3 * (1 - \psi_2)$	0	0
$\phi_1 * \psi_1$	0	0	0	0
0	$\phi_2 * \psi_2$	$\phi_3 * \psi_2$	ϕ_2	ϕ_3

According to the best model resulting from multi-event modelling (see the Results section), the matrix was structured in three age classes for survival probability (coded as ϕ_1 , ϕ_2 and ϕ_3) and two age classes (1 and 2 years old or older) for recruitment probability (coded as ψ_1 and ψ_2). The matrix was organized as: newborn individuals, 1-year-old non-breeder individuals, 2-year-old and older non-breeder individuals, 1-year-old breeder individuals, 2-year-old and older breeder individuals. We assumed that as soon as an individual has recruited in the population, it breeds every year. f is fecundity expressed as the number of chicks per pair.

In the first step, we calculated the eigenvalue, λ , of the matrix (Caswell, 2001) using the output of the multi-event modelling for ϕ , ψ and f . In the second step, we iteratively changed the fecundity rates in the matrix so that the

Table 1 Model selection for apparent survival (ϕ), first recruitment (r) and recapture rates (p) for all chicks ringed in the Camargue between 1997–2010 ($n = 3408$)

Model	ϕ	r	p	N° Par	Deviance	Δ QAICc
11	$a_1^*t + a_2 + a_3$	a_2	hc^*t	58	10 089.5	0
6	$a_1^*t + a_2 + a_3$	a_3	hc^*t	58	10 090.14	2.67
9	$a_1^*t + a_2$	a_3	hc^*t	57	10 110.77	21.26
7	$a_1^*t + a_2^*t + a_3$	a_3	hc^*t	69	10 093.86	28.83
5	a_3^*t	a_3	hc^*t	78	10 076.88	30.27
8	t	a_3	hc^*t	55	10 325.55	231.98
3	a_3^*t	a_3	$a_2^*hc^*t$	79	10 676.26	631.7
1	a_3^*t	a_3^*t	$a_2^*hc^*t$	111	10 615.18	636.54
4	a_3^*t	a_3	a_2^*hc	43	10 786.2	668.25
2	a_3	a_3^*t	$a_2^*hc^*t$	78	10 843.59	796.98
10	$a_1^*t + a_2 + a_3$	a_3	t	31	10 952.52	810.29

a indicates the age class with the number of age classes considered for each parameter noted in the subscript; t denotes a temporal effect; hc denotes a heterogeneity class effect on recapture probability. Δ QAICc indicates the difference in QAICc values between models. Individuals transition rates (tr) between heterogeneity classes was considered constant in all models.

modelled λ matched those observed for the 1973–1997 and 1997–2010 periods. To do this, we considered the mean estimated survival and recruitment probabilities or the upper limit of their confidence intervals. In the third step, we conducted the same type of analysis using the observed mean fecundity and testing varying survival probabilities. Lastly, we refined the matrix model to include an immigrant class following Sarrazin & Legendre (2000): the number of females that would need to immigrate to the population every year to match the observed population growth rate was estimated by an iterative process. In this model, immigrants were considered as females adults (see ESM-2). We assumed no counting errors in the estimation of population size. Because of the low-estimated adult survival (see the Results section) compared to the black-headed gull, a gull of similar size, we hypothesized that some individuals permanently emigrate from the French population. In order to evaluate whether the population is stable at a larger scale, we estimated the number of immigrants needed to obtain the observed growth rate by using the black-headed gull adult estimate of survival (0.90; Prévot-Julliard *et al.*, 1998) and keeping all other parameters the same as in the previous modelling. By doing so, we simulated a situation where the permanent emigration would be nul, thus permitting the estimation of pure immigration at a larger scale.

Results

Capture–recapture analysis

The best model (model 11; Table 1) considered three age classes for survival and two age classes for recruitment probabilities. Survival varied significantly over time in the first year of the individuals (Fig. 2) and was constant for 2-year and 3-year or older individuals (denoted in the models as a_2

Table 2 Parameter estimates as resulted from the best model (model 11), for apparent survival (ϕ), first recruitment (r) and recapture rates (ρ) and transition probability between classes of recapture heterogeneity (tr) for all chicks ringed in the Camargue between 1997–2010 ($n = 3408$)

Parameters	Class	Estimates	CI-	CI+	SE
ϕ	2 years old	0.70	0.61	0.78	0.04
ϕ	≥ 3 years old	0.81	0.79	0.83	0.01
r	1 year old	0.10	0.08	0.12	0.01
r	≥ 2 years old	0.41	0.37	0.45	0.02
tr	Constant	0.99	0.97	1.00	0.01

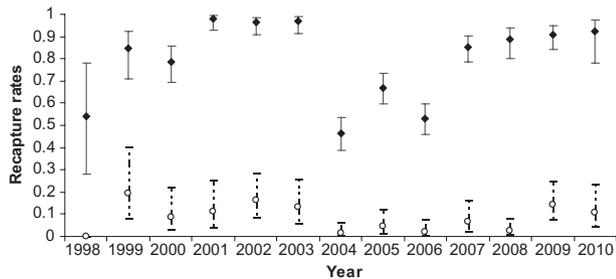


Figure 3 Recapture rates according to heterogeneity class: recapture rates of B+ are shown in black filled diamonds and of that of B- are shown in open dots. 95% confidence intervals are also shown for the two classes (in solid and dashed lines, respectively).

and a_3 , respectively), with survival rates equal to 0.70 (0.61–0.78) and 0.81 (0.79–0.83), respectively (Table 2). Recruitment probability was estimated at 0.10 (0.08–0.12) for 1-year-old individuals and at 0.41 (0.37–0.45) for birds ≥ 2 years old. Resighting probability differed for B+ and B- classes, confirming the presence of resighting heterogeneity among individuals (model 6 vs. model 10; Table 1). Temporal variations of resighting probabilities for the two HC are shown in Fig. 3. The probability of one bird to remain in B+ or B- was very high, equal to 0.99 (0.97–1).

Fecundity

A total of 69 colonies were monitored between 1997 and 2010. The fecundity was highly variable, ranging from zero (complete failure for 43% of the colonies) to 1.96 chicks per pair. Colony fecundity rates over time are shown in Fig. 2b. Overall, the mean fecundity of the French population of the slender-billed gull between 1997 and 2010 was 0.66 (0.47–0.85) chicks per pair.

Population size and growth rate estimated from breeding counts

Using count data of breeders over the whole French Mediterranean coast (Fig. 1), the observed annual growth rate varied according to the period considered. It was estimated at $\lambda_{obs} = 1.09$ (0.94–1.26) over the whole 1973–2010 period,

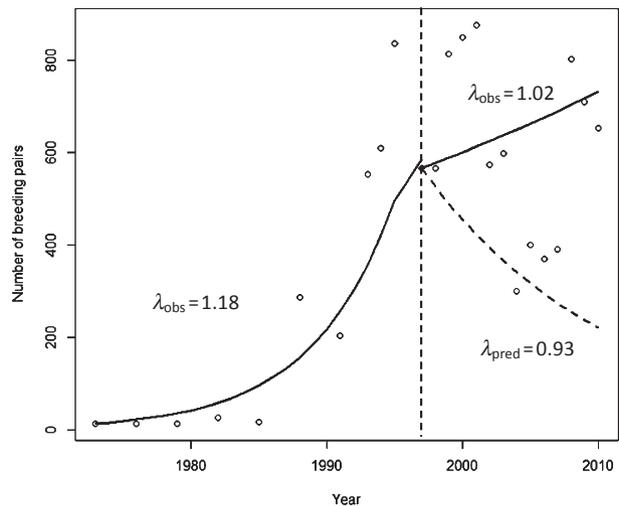


Figure 4 Observed (dots) and modelled evolution of slender-billed gull *Larus genei* breeding numbers between 1973 and 2010 in southern France. Plain lines are the fitted growth curves according to the estimated growth rate for the 1973–1997 and 1997–2010 periods; the dotted line is the fitted growth curve according to the growth rate estimated by the matrix model using the output of multi-event modelling for the 1997–2010 period only.

$\lambda_{obs} = 1.18$ (0.95–1.46) between 1973 and 1997, and $\lambda_{obs} = 1.02$ (0.99–1.48) between 1997 and 2010 (Figs 2 and 4).

Population dynamics modelling

The stochastic annual growth rate simulated from the stochastic population matrix modelling was 0.93 over the period 1997–2010, predicting a sharp decline in population size (Figs 2 and 4). This was considerably lower than the λ observed over the whole period of 1973–2010 ($\lambda_{obs} = 1.09$) and also lower than that observed over the 1997–2010 period ($\lambda_{obs} = 1.02$).

When considering the mean estimated survival rates, 1.28 chicks per pair would be required in order to reach the actual growth rate of the 1997–2010 period, that is, a fecundity 1.94 times higher than that observed. To reach the λ estimated for the 1973–1997 period, 2.77 chicks per pair would be required, that is, 4.20 times the observed value.

With the survival and recruitment probabilities fixed at the upper limit of their confidence intervals, mean fecundity values of 0.78 and 1.73 chicks per pair would be necessary to match the observed λ for the periods of 1997–2010 and 1973–97, respectively, that is, 1.2 times and 2.62 times those observed.

If we fix the fecundity rate to the observed value, the adult survival probability has to be fixed to 0.90 to obtain the λ estimated over the period 1997–2010. The adult survival probability has to be fixed to 0.97 to obtain the λ estimated for the period 1973–1997.

Immigration

When the demographic parameters are fixed to their estimated values, an average of 66 females would have to

immigrate to the French population annually to fit the population growth rate of the 1973–1997 period. Over the 1997–2010 period, 57 female immigrants would be necessary annually to reach the observed $\lambda = 1.02$. Fixing the adult survival equal to the black-headed gull estimate (0.90), the mean number of yearly female immigrants was estimated to 19.5 over the first period and only 0.5 over the second period.

Discussion

Contrasting matrix modelling (built with local demographic parameter estimates) with count data suggests that the sharp increase of the slender-billed gull population observed in France in the 1980s and 1990s, as well as its relative stability observed over the last 15 years, cannot be achieved only by intrinsic dynamics. As previously suspected (Sadoul, 1997), our study supports the hypothesis that the current status of the French population of the species is highly dependent on immigration from other populations. Several studies have shown that the spatial scale at which population dynamics operate were larger than generally thought (e.g. Mayer, Schiegg & Pasinelli, 2009; Schaub *et al.*, 2012); however, the spatial scale considered here is much larger than usually considered (but see Balkiz *et al.*, 2010) and allow inferring the functioning of a population at the Mediterranean scale.

This paper provides the first survival probability estimates for slender-billed gulls. First-year local survival probability varied over time and was, on average, similar to that of the black-headed gull (Prévot-Julliard, 1996). However, adult survival probability of slender-billed gulls was considerably lower than that of other Larids of similar size – about 10% lower than that of the black-headed gull (Prévot-Julliard *et al.*, 1998). Larid species are characterized by longevity and have only few predators. To our knowledge, the slender-billed gulls do not depart from this scheme and we never observed any case of adult predation. It is more likely that such a low local survival rate results from permanent emigration from its natal area, although we cannot totally exclude mortality risk outside the French sites, particularly along migration journeys. We used the probability of accessing the breeding colony as a proxy for the recruitment rate. Even though this approach may bias high recruitment probability, the estimate remained very low for first-year birds (0.10), suggesting that a large majority of slender-billed gulls do not breed before they are 2 years old, as observed in the field (N. Sadoul and C. Pin, pers. obs.). This is consistent with the biology of other small gulls (Cramp & Simmons, 1985; del Hoyo *et al.*, 1996; Schreiber & Burger, 2002). Access to the breeding site for 2-year-old or older breeders, that is, 0.41 (0.37–0.45), was also very close to that of black-headed gulls (0.38) (Torcel, 2001). This suggests that our measure of recruitment is probably realistic and not too overestimated.

The fecundity of slender-billed gulls in France is characterized by a high probability of complete breeding failure as 43% of colonies did not produce any young. This is much higher than in the black-headed gull, for which only 17% of the colonies showed complete failure (Gonzales-Davila,

1994). In the black-headed gull, mean fecundity ranges from 0.66 to 2.11 chicks per pair, depending on year and location (Grosbois, 2001; Lebreton & Isenmann, 1976; Lebreton & Landry, 1979; Prévot-Julliard, 1996; Viksne, 1980), and is thus systematically higher than the mean fecundity observed in our slender-billed gull population (0.66). In Spain, slender-billed gulls had an average breeding success of 0.71 (Oro, 2002), which is of the same order than that of our study sites. Most of the colony sites used by the species in France are accessible to terrestrial predators, and this vulnerability may explain the low fecundity and the high frequency of complete failure. However, in long-lived species such as Larids, population dynamics are not very sensitive to variations in fecundity (Saether & Bakke, 2000), yet, massive failures can induce dispersal (Oro, Pradel & Lebreton, 1999). Studies on Mediterranean gull populations have stressed the importance of immigration on the dynamics of local colonies (Oro & Pradel, 1999; Oro & Ruxton, 2001; Martínez-Abraín *et al.*, 2003; Cam *et al.*, 2004). The frequent reproductive failure observed in France may thus promote long-distance permanent emigration, which, in turn, may explain the low estimate of local survival.

Using the estimated demographic parameters of the local population, the calculated annual growth rate of the French population of the slender-billed gull was 0.93, suggesting a sharp population decline. Yet, this contrasts with the relatively stable trend in population size observed since the beginning of the ringing–resighting programme ($\lambda_{obs} = 1.02$). The output of our matrix population modelling may be biased by (1) the use of an average fecundity rate while the data suggest large annual variations of fecundity across years and (2) by the use of an indirect measure of recruitment. Highly variable fecundity rates generally decrease the net growth rate of the population in projected population models (Caswell, 2001), and as mentioned earlier, access to the breeding site may be viewed as the upper limit of true recruitment. Hence, if the calculated annual growth rate is biased, it should be overestimated rather than underestimated, and thus the discrepancy between the predicted and observed growth rate may be even higher than the one demonstrated in this study.

The extremely high growth rate observed in the 1980s and 1990s cannot be realistically explained solely by local population dynamics. One of the main avian predators of slender-billed gull offspring, the yellow-legged gull *Larus michahellis*, was less abundant during the period of exponential increase of slender-billed gull numbers (1985–1997) (Sadoul *et al.*, 1996). Yet, even if fecundity was higher during this period, it would have to have risen to 2.60 fledging chicks per pair to fit the observed growth rate, which remains unrealistic for a Larid species. Similarly, to fit the growth rate observed before 1997, the survival probability would have to have risen to 0.97 for all age classes. Such demographic parameters are unrealistic and significantly higher than any observed, even for large gulls during phases of expansion (Schreiber & Burger, 2002). Extrinsic factors at the meta-population level can play a significant role in local dynamics. Our study indicates that the estimated number of

female adults permanently immigrating to France every year was between 66 and 57 female individuals, depending on the period; a very large proportion of the population during the first period (1973–1997) and about 10% of the current population size.

The existence of a stable and long-term heterogeneity in resighting probability, with some birds systematically difficult to observe and others with a high probability of being observed from one year to another, despite the high observation pressure in France, is intriguing. Indeed, the location of the colonies change every year and it is thus impossible that some birds systematically breed in colonies where detection is low because such low detection colonies are very rare. Because permanent emigration is already taken into account in survival probability, we suspect that this phenomenon is related to individual variation in site fidelity: site-faithful birds are observed almost every year in France, while others may be present only in certain years, either because they breed elsewhere or because they skip reproduction in some years. Such temporary emigration does not bias survival probability (Kendall & Nichols, 1995). Hence, temporary emigration is not responsible for the large number of immigrants necessary to compensate for the low local survival probability (discussed below). However, the existence of individuals being irregularly present in the Camargue reinforces the idea that the slender-billed gull population dynamics largely depend on the emigration–immigration process, with some individuals exhibiting back and forth movements in and out of the south of France. Indeed, chicks ringed in Spain and Italy are regularly resighted in France and vice versa (N. Sadoul and C. Pin, pers. Obs.). Population size fluctuations have been reported for this species in Spain by Oro (2002), who also concluded that these fluctuations may be generated by emigration–immigration processes at the meta-population level, without being able to quantify it. Strong population's fluctuations, such as the ones observed in our study area, seem to be typical of the species, probably resulting from disequilibrium between temporary emigration and immigration processes during some years. The mechanisms that drive these fluctuations and their relation to evolution and population dynamics issues should be further studied. Comparative analyses of the local population numbers in France, Spain, Italy and also in North Africa would provide further insight on the potential exchanges between populations, in case of synchronous local increase/decrease rates observed in different breeding populations.

Despite the fact that the French population was clearly flowed in by other populations by permanent immigration process, especially until late 1990s, the low local survival probability suggests that the French population also exports individuals (see previous discussion). By simulating the absence of permanent emigration using a high adult survival probability, that is, 0.9, we estimated that the pure immigration was about 20 females over the first period, that is, before 1997, but negligible (0.5) during the period 1997–2010. If our simulation is indeed a good proxy of the true survival rate, these results suggest that over the last decade,

the population of the slender-billed gull may have been relatively stable and that the French population may no longer act as a sink population as it may export as many individuals as it imports. We should note, however, that any decrease in fecundity or in adult survival rates would lead to a decline in breeding numbers, setting new emigration/immigration equilibrium.

Yet, the importance of the exchange between (sub)population of the slender-billed gulls suggests that the viability and conservation of the French population cannot be considered independently from other populations of this species. Consequently, effective conservation plans would need to be implemented at a much larger scale than nationally. However, we do not know with certainty where the birds in the French subpopulation come from, nor where the emigrants go to. The population increase observed in France over the 1985–2000 period matches that observed elsewhere in the western Mediterranean (Isenmann & Goutner, 1993). Installations of some colonies were also reported in North Africa in the 1980s (Chokri, Hammouda & Tavecchia, 2011), and numbers in the Sfax salt pans in Tunisia have expanded enormously since 1985 (Amis des Oiseaux Association, unpubl. data). Our results suggest that the increase in France was induced by a permanent pure immigration (39 individuals every year). This result may be the rule for the whole Western expansion. Immigrants may come from the Black Sea area, where populations have exhibited a dramatic decline since 1985 as a result of the degradation of their foraging habitat (Rudenko, 1996). Although the French population is probably no longer a sink population, it does not necessarily imply that all the Western population is stable. Indeed, some large populations, for instance, those of North Africa, may still be flowed in by individuals from the Black Seas area. To develop an efficient conservation strategy for the species, we now need more insights on the population dynamic of all the (sub)populations of the Mediterranean basin including the Black Sea population. A coordinated capture-mark-recapture (CMR) programme is thus crucial to better understand the dynamics of the species and to better assess its conservation status. Regarding the western Mediterranean, the slender-billed gull's breeding habitats, that is, lagoons and salt pans, are threatened by the increasing urbanization of the coast and the abandonment of salt pans (Béchet *et al.*, 2012). So paradoxically, local population increase may not be a sign of the species' good health, but reflect large-scale population problems (Sadoul, 1997, 1998). The significant colonization/extinction dynamic observed at an intra-regional scale and the large between-year fluctuations of population sizes observed at a larger scale probably necessitate the protection of a maximum number of potential breeding sites. This is only possible to achieve through coordinated international action.

Conclusion

In conclusion, our study demonstrates that the status and dynamics of a single population, even one that largely

depends on its exchanges with other subpopulations, can be assessed using well-known demographic tools, such as ring-resighting analysis and basic matrix population models. From a conservation point of view, we identified that at the local scale, any decrease of fecundity or an adult survival rate lower than 0.9 would lead to populations that rely more on emigration/immigration equilibrium than on intrinsic dynamics. However, at the west Mediterranean scale, the slender-billed gull population is probably less threatened than first thought at least over the western part of their distribution. Our approach is fairly general and easy to implement and may be applicable to most species for which counts and demographic parameters are available.

Acknowledgements

We would like to thank the Tour du Valat Research Center and the association of Amis des Marais du Vigueirat which support the CMR programme. We thank Heinz Hafner for the initiative of the slender-billed gull CMR programme in France. We also thank Michael Schaub, Daniel Oro and one anonymous reviewer for their comments on a previous version of this work. This study was funded by the Foundation MAVA, which provided financial support to the long-term study and by the Ecole Pratique des Hautes Etudes.

References

- Akçakaya, H.R. (2000). Viability analyses with habitat-based metapopulation models. *Popul. Ecol.* **42**, 45–53.
- Balkız, Ö., Béchet, A., Rouan, L., Choquet, R., Germain, C., Amat, J.A., Rendón-Martos, M., Baccetti, N., Nissardi, S., Özemesi, U. & Pradel, R. (2010). Experience-dependent natal philopatry of breeding greater flamingos. *J. Anim. Ecol.* **79**, 1045–1056.
- Béchet, A., Rendón-Martos, M., Rendón, M.A., Amat, J.A., Johnson, A.R. & Gauthier-Clerc, M. (2012). Global economy interacts with climate change to jeopardize species conservation: a case study in the greater flamingo in the Mediterranean and West Africa. *Environ. Conserv.* **39**, 1–3.
- Burnham, K.P. & Anderson, D.R. (2002). *Model selection and multi-model inference*. 2nd edn. New York: Springer-Verlag.
- Cam, E., Oro, D., Pradel, R. & Jimenez, J. (2004). Assessment of hypotheses about dispersal in a long-lived seabird using multistate capture-recapture models. *J. Anim. Ecol.* **73**, 723–736.
- Caswell, H. (Ed.) (2001). *Matrix population models: construction, analysis and interpretation*. Sunderland, MA: Sinauer Associates.
- Chokri, M.A., Hammouda, A. & Tavecchia, G.O. (2011). Survival of slender-billed gull chicks during the crèching period. *Bird Study* **58**, 443–449.
- Choquet, R., Lebreton, J.D., Gimenez, O., Reboulet, A.M. & Pradel, R. (2009a). U-care: utilities for performing goodness of fit tests and manipulating capture-recapture data. *Ecography* **32**, 1071–1074.
- Choquet, R., Rouan, L. & Pradel, R. (2009b). Program e-surge: a software application for fitting multievent models. *Environ. Ecol. Stat.* **3**, 845–865.
- Clobert, J., Lebreton, J.D., Allainé, D. & Gaillard, J. (1994). The estimation of age-specific breeding probabilities from recaptures or resightings of marked animals. II. Longitudinal models. *Biometrics* **50**, 375–387.
- Cramp, S. & Simmons, K.E.L. (1985). *Handbook of the birds of Europe, the Middle East and North Africa. The birds of the Western Palearctic*. Oxford: Oxford University Press.
- Crooks, K. & Sanjayan, M. (2006). *Connectivity conservation*. Cambridge: Cambridge University Press.
- Del Hoyo, J., Elliot, A. & Argatal, J. (1996). *Handbook of the birds of the world*. Barcelona: Lynx Edicions.
- Drechsler, M., Frank, K., Hanski, I., O'Hara, R.B., & Wissel, C. (2003). Ranking metapopulation extinction risk: from patterns in data to conservation management decisions. *Ecol. Appl.* **13**, 990–998.
- Gonzales-Davila, G. (1994). *Démographie animale et biologie des populations. Modélisation et applications à la gestion d'espèce sauvages*. Université Montpellier II.
- Grosbois, V. (2001). *La dispersion: Trait d'histoire de vie et paramètre démographique. Etude empirique dans une population de mouette rieuse larus ridibundus I*. Université Montpellier II.
- Gyllenberg, M. & Hanski, I. (1997). Habitat deterioration, habitat destruction, and metapopulation persistence in a heterogenous landscape. *Theor. Popul. Biol.* **52**, 198–215.
- Hanski, I. & Gilpin, M.E. (1997). *Metapopulation dynamics: ecology, genetics and evolution*. London: Academic Press.
- Isenmann, P. (1976). Contribution à l'étude de la biologie de la reproduction et de l'étho-écologie du goéland railleur, *Larus genei*. *Ardea* **64**, 48–61.
- Isenmann, P. & Goutner, V. (1993). Breeding status of the slender-billed gull (*larus genei*) in the Mediterranean basin. In *Status and conservation of seabirds*: 65–70.
- Aguilar, J.S., Montbailliu, X. & Paterson, A.M. (Eds). Madrid: SEO/birdlife/medmaravis.
- Isenmann, P. & Sadoul, N. (1999). Le goéland railleur, *Larus genei*. In *Oiseaux menacés et à surveiller en France. Listes rouges et recherche de priorités*: 244–245.
- Rocamora, G. & Yeatman-Berthelot, D. (Eds). Paris: Société d'Etudes Ornithologiques de France/Ligue pour la protection des Oiseaux.
- Kendall, W.L. & Nichols, J.D. (1995). On the use of secondary capture-recapture samples to estimate temporary emigration and breeding proportions. *J. Appl. Stat.* **22**, 751–762.
- Kleinhans, D. & Jonsson, P.R. (2011). On the impact of dispersal asymmetry on metapopulation persistence. *J. Theor. Biol.* **290**, 37–45.

- Lebreton, J.D., Burnham, K.P., Clobert, J. & Anderson, D.R. (1992). Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol. Monogr.* **62**, 67–118.
- Lebreton, J.D. & Clobert, J. (1991). Bird population dynamics, management, and conservation: the role of mathematical modelling. In *Bird population studies, relevance to conservation and management*: 105–125. Perrins, C.M., Lebreton, J.D. & Hiron, G.J.M. (Eds). Oxford: Oxford university Press.
- Lebreton, J.D. & Isenmann, P. (1976). Dynamique de la population camarguaise de mouette rieuse: un modèle mathématique. *Terre et Vie* **30**, 529–549.
- Lebreton, J.D. & Landry, P. (1979). Fécondité de la mouette rieuse, *larus ridibundus*, dans une colonie importante de la plaine du forez (Loire, France). *Le Gerfaut* **69**, 159–194.
- Martínez-Abraín, A., Oro, D., Forero, M.G., & Conesa, D. (2003). Temporal and spatial local population dynamics in a long-lived seabird. *Popul. Ecol.* **45**, 133–139.
- Mayer, C., Schiegg, K. & Pasinelli, G. (2009). Patchy population structure in a short-distance migrant: evidence from genetic and demographic data. *Mol. Ecol.* **18**, 2353–2364.
- Morris, W.F. & Doak, D.F. (Eds) (2002). *Quantitative conservation biology: theory and practice of population viability analysis*. Sunderland, MA: Sinauer Associates.
- Navarro, J., Oro, D., Bertolero, A., Genovart, M., Delgado, A. & Forero, M.G. (2010). Age and sexual differences in the exploitation of two anthropogenic food resources for an opportunistic seabird. *Mar. Biol.* **157**, 2453–2459.
- Nicol, S.C., Chadès, I., Linke, S. & Possingham, H.P. (2010). Conservation decision making in large state spaces. *Ecol. Modell.* **221**, 2531–2536.
- Oro, D. (2002). Breeding biology and population dynamics of slender-billed gulls at the ebro delta (northwestern Mediterranean). *Waterbirds* **25**, 67–77.
- Oro, D. & Pradel, R. (1999). Recruitment of Audouin's gull to the Ebro Delta colony at metapopulation level in the western Mediterranean. *Mar. Ecol. Prog. Ser.* **180**, 267–273.
- Oro, D. & Ruxton, G.D. (2001). The formation and growth of seabird colonies: audouin's gull as a case study. *J. Anim. Ecol.* **70**, 527–535.
- Oro, D., Pradel, R. & Lebreton, J.D. (1999). The effects of nest predation and food availability on life history traits in audouin's gull. *Oecologia* **118**, 438–445.
- Peery, M.Z., Becker, B.H. & Beissinger, S.R. (2006). Combining demographic and count-based approaches to identify source–sink dynamics of a threatened seabird. *Ecol. Appl.* **16**, 1516–1528.
- Peron, G., Crochet, P.A., Choquet, R., Pradel, R., Lebreton, J.D. & Gimenez, O. (2010a). Capture-recapture models with heterogeneity to study survival senescence in the wild. *Oikos* **119**, 524–532.
- Peron, G., Lebreton, J.-D. & Crochet, P.-A. (2010b). Breeding dispersal in black-headed gull: the value of familiarity in a contrasted environment. *J. Anim. Ecol.* **79**, 317–326.
- Pradel, R. (1993). Flexibility in survival analysis from recapture data, handling trap-dependence. In *Marked individuals in the study of bird population*: 29–37. Lebreton, J.-D. & Nroth, P. (Eds). Basel: Birkhäuser.
- Pradel, R. (2005). Multievent: an extension of multistate capture-recapture models to uncertain states. *Biometrics* **61**, 442–447.
- Pradel, R., Hines, J.E., Lebreton, J.D. & Nichols, J.D. (1997a). Capture–recapture survival models taking account of transients. *Biometrics* **53**, 60–72.
- Pradel, R., Johnson, A.R., Viallefont, A., Nager, R. & Cézilly, F. (1997b). Local recruitment in the greater flamingo: a new approach using capture-mark-recapture data. *Ecology* **78**, 1431–1445.
- Pradel, R. & Lebreton, J.D. (1999). Comparison of different approaches to the study of local recruitment of breeders. *Bird Study* **46** (Suppl.), 74–81.
- Prévoit-Julliard, A.-C. (1996). *Rôle de la dispersion dans la dynamique d'une population de mouette rieuse larus ridibundus*. Université de Montpellier II.
- Prévoit-Julliard, A.C., Lebreton, J.D. & Pradel, R. (1998). Re-evaluation of adult survival of black-headed gulls (*larus ridibundus*) in presence of recapture heterogeneity. *Auk* **115**, 85–95.
- Radchuk, V., Wallisdevries, M.F. & Schtickzelle, N. (2012). Spatially and financially explicit population viability analysis of *Maculinea alcon* in the netherlands. *PLoS ONE* **7** (6): e38684. (online DOI: 10.1371/journal.pone.0038684)
- Reed, J.M., Mills, L.S., Dunning, J.B., Menges, E.S., McKelvey, K.S., Frye, R., Beissinger, S.R., Anstett, M. & Miller, P. (2002). Emerging issues in population viability analysis. *Conserv. Biol.* **16**, 7–19.
- Ross, J.V. & Pollett, P.K. (2010). Simple rules for ranking and optimally managing metapopulations. *Ecol. Modell.* **221**, 2515–2520.
- Rudenko, A.G. (1996). Present status of gulls and terns nesting in the back sea biosphere reserve. *Colon. Waterbird* **19**, 41–45.
- Sadoul, N. (1996). *Dynamique spatiale et temporelle des colonies de charadriiformes dans les salins de Camargue: implication pour la conservation*. Montpellier: Université Montpellier II.
- Sadoul, N. (1997). The importance of spatial scales in long-term monitoring of colonial charadriiformes in southern France. *Colon. Waterbirds* **20**, 330–338.
- Sadoul, N. (1998). Expansion des laridés en camargue: populations en bonne santé ou dysfonctionnement? In: *Actes du 36ème Colloque interrégional d'Ornithologie. Nos Oiseaux* **45** (Suppl. 2), 83–86. Neuchâtel.

- Sadoul, N., Johnson, A.R., Walmsley, J.G. & Leveque, R. (1996). Changes in the number and the distribution of colonial charadriiformes breeding in the Camargue, southern France. *Colon. Waterbirds* **19**, 46–58.
- Saether, B.E. & Bakke, O. (2000). Avian life history variation and contribution of demographic trait to the population growth rate. *Ecology* **81**, 642–653.
- Sarrazin, F. & Legendre, S. (2000). Demographic approach to releasing adults versus young in reintroductions. *Conserv. Biol.* **14**, 488–500.
- Schaub, M., Reichlin, T.S., Abadi, F., Kéry, M., Jenni, L. & Arlettaz, R. (2012). The demographic drivers of local population dynamics in two rare migratory birds. *Oecologia* **168**, 97–108.
- Schreiber, E.A. & Burger, J. (2002). *Biology of marine birds*. Boca Raton: CRC Press.
- Torcel, L. (2001). *Etude de la dynamique d'une population de mouette rieuse (larus ridibundus) par l'analyse conjointe de recaptures et de reprises*.
- Van Teeffelen, A., Cabeza, M. & Moilanen, A. (2006). Connectivity, probabilities and persistence: comparing reserve selection strategies. *Biodivers. Conserv.* **15**, 899–919.
- Viksne, J.A. (1980). Some problems in the black-headed gull *Larus ridibundus* research and the necessity of international cooperation in this respect. *Acta Ornithol.* **17**, 71–80.

Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Matrixes used for multievent capture–recapture analysis in E-Surge.

Appendix S2. Leslie matrix including immigrants.

Appendix S3. R code to estimate the number of immigrants for deterministic matrix models.