

Dynamics of a northern fulmar (*Fulmarus glacialis*) population at the southern limit of its range in Europe

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Abstract In the context of global changes, defining the source–sink dynamics of populations of emblematic species, such as seabirds, within the limits of their distribution range is often crucial to optimize the priorities of surveys and conservation management, especially in protected areas. However, ringing is often not possible and only simple survey methods, such as the ‘apparently occupied sites’ method, can be utilized by managers of protected areas and threatened species. Using data collected between 1997 and 2005, we investigated the population dynamics of the northern fulmar (*Fulmarus glacialis*) at the southern limit of its range on the western French coast, which hosts increasing populations. Using a robust design spatial occupancy model, we estimated the proportion of occupied nests, the rates of nest colonization, nest extinction and the population growth rates of four colonies of the largest population (Ouessant Island). The estimated annual growth rate was high (average 1.049). A deterministic population dynamics model indicated that the observed rapid increase of Ouessant populations cannot be explained by their intrinsic dynamics, which suggested an important role for immigration. Different demographic scenarios provide several lines of evidence that the large northern fulmar population in this Man and Biosphere Reserve is a sink population. The strong increase in a population located at the limits of the species distributional range implies that it functions as a population sink. Inexpensive effective

survey methods could allow investigation of the demographic status of seabird populations and provide relevant information for the hierarchization of conservation priorities.

Keywords Colony growth · Immigration · Matrix model · Robust design occupancy estimation · Seabird surveys

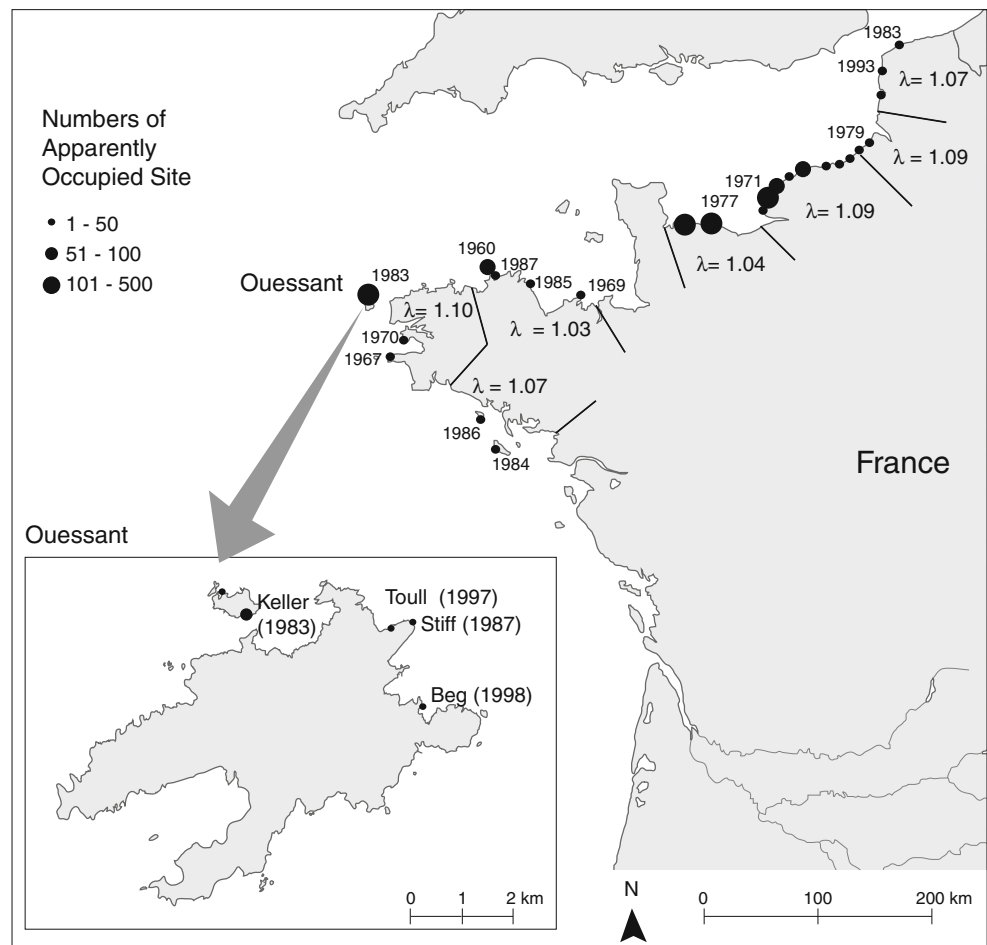
Introduction

In species that naturally occur in patchy or fragmented habitats, dispersal plays a major role in global dynamics via its effects on both local dynamics (Johst and Brandl 1997) and recolonization rates and patterns (Hanski 1998). In metapopulations, the relative contributions of the demographic processes underlying temporal variations in local population sizes (e.g., reproduction and immigration) are expected to vary according to the location of populations (i.e., populations at the core vs. the border of the species range; Holt and Keitt 2005). Range limits may be caused by gradients in extinction rates, colonization rates or habitat availability. Theoretical models have predicted that recurrent immigration from source populations can inflate the size of the realized range by maintaining a species at sites with unfavorable niche conditions (Pulliam 2000; Holt et al. 2005). On the basis of theoretical expectations, in central habitat sites, local populations should be intrinsically and deterministically increasing (‘source populations’), whereas the opposite may occur in marginal habitats (‘sink populations’; see Pulliam 1988). In seabirds, several empirical studies have indeed shown that intrinsic dynamics do not always sustain local populations and that immigration can substantially improve population growth rate (Ollason and Dunnet 1983; Porter and Coulson

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Fig. 1 French northern fulmar breeding colony sizes expressed as number of apparently occupied sites, their date of establishment and the average growth rate for each littoral department assessed for the period 1978–1998 (from Cadiou and Lang 2004)



1987; Ainley et al. 1990; Danchin and Monnat 1992; Morais et al. 1998; Oro and Ruxton 2001). Although sink populations are unable to persist in the absence of immigration, they may contribute to metapopulation size and persistence (Howe et al. 1991). In species with patchy distributions, assessment of the status of local populations in terms of the source–sink dichotomy is therefore of primary importance to understand the species' dynamics and has strong implications for local and global conservation. Furthermore, the evolution of range limits is currently understudied (Sexton et al. 2009), while is a field that could be crucial, especially in the context of global changes (climate, food availability, etc.).

If estimation of the relative importance of immigration and natural growth rate is crucial, it is necessary to collect data for the estimation of demographic parameters, which raises several problems: in many instances, because of time and technical limitations, ringing surveys are not feasible and only simple, cost-effective methods, such as surveys of site occupancy, can be utilized by managers of protected areas and threatened species. However, few studies have used such data to address the processes underlying the source–sink dynamics of seabird populations despite their

usefulness. Recent development of powerful statistical methods to analyze such kinds of data would allow managers to assess population sizes and trends.

The issues of assessing population demographics and the technical limits linked to ringing are especially pertinent for the long-lived seabird, the northern fulmar (*Fulmarus glacialis*), which reaches the extreme southern limit of its range in Europe. The species has been established in France since 1960 and has progressively colonized a large portion of the northern French coastline, with all monitored populations deterministically increasing (deterministic growth rate [λ] higher than one) from 1978 to 1998 (mean 1.06, range 1.03–1.10) (Fig. 1; Cadiou and Lang 2004). This trend is shown especially by the population that colonized the island of Ouessant off the western coast of Brittany, France. This population was established in 1983 and grew dramatically such that, by 2005, this population represented 15% of the total French population. However, as in many cliff-nesting seabirds, individual marking is constrained because of the difficulty of accessing nests. Moreover, in Procellariidae species, resightings of marked birds are hindered owing to their inability to stand up on their legs. In the absence of

individual life history data, we used survey data to develop two different estimates for the local population growth rate. Comparison of these estimates allowed us to evaluate the relative effects of intrinsic processes and dispersal on population growth. As a first step, surveys of Ouessant Island colonies undertaken between 1997 and 2005 allowed us to estimate the annual probability of persistence of occupied nests, the annual rate of nest colonization, nest extinction and the growth rate of the pool of effective breeders using robust design spatial occupancy models (MacKenzie et al. 2003; see also Bled et al. 2011 for a case study of a colonial seabird population). Secondly, we developed a deterministic age-classified population dynamics matrix model to examine the effects of various demographic parameters on population growth. In particular, the model was implemented with (1) a combination of specific parameters (reproductive success estimated for the Ouessant population) and parameters obtained from the literature (this model assumes no immigration) and (2) the demographic parameters previously estimated with the robust design spatial occupancy model. Comparison of these models and the estimates of colony growth rates permitted evaluation and discussion of the contribution of immigration to the apparent local growth rate.

Methods

Study area

The northern fulmar became established along the French coast only in recent decades; breeding events were first confirmed in 1960 in Les Sept Iles, Brittany, France, and establishment of the species on Ouessant's cliffs was noted in 1983 (Cadiou and Lang 2004; Fig. 1). The current distribution of the species is discontinuous, and Brittany is the southern limit of its European range. Ouessant is located 20 km west of the western coast of Brittany, France (48°28'N, 5°5'W; Fig. 1). On the basis of the presence of rare species, high biological diversity and an exceptionally preserved coastal ecosystem, this island is listed in national and European inventories, e.g., as an International Bird Area and in the Natura 2000 reserve network, and the island has been part of a Natural Regional Park since 1969 and became a Man and Biosphere Reserve in 1988 and a National Park in 2007. Seabird colonies are considered to be the core of this natural heritage.

Northern fulmar monitoring

To investigate the dynamics of the northern fulmar population of Ouessant, we used data obtained by colony

surveys conducted between 1997 and 2005. The Ouessant population comprises several colonies (Fig. 1), and only colonies that could be seen easily from the coast were monitored. These colonies—Beg, Toull, Stiff and Keller—comprise more than 90% of breeding fulmar sites on Ouessant (Audevard 2007). All nest sites in these four colonies were monitored during the study period. Nests were identified each year using a database of photographs of cliffs and each nesting site was designated with a specific code. The use of codes and photographs was consistent throughout the study period to avoid misidentification of individual sites (an example of a photograph of a cliff is presented in Appendix S1 in Electronic Supplementary Material (ESM).

During the breeding period, which extended from May (the beginning of egg laying) to early September (the end of fledging), all sites were checked and numbers of adults, eggs and chicks were recorded until fledging. However, the lack of built nests, the presence of non-breeders in colonies, and the low detectability of eggs and young chicks hindered a precise estimation of the number of breeders. We therefore focused our study on nest occupancy from 19 May to 31 July in each year, which is a period characterized by a high attendance of breeders and a relatively low presence of non-breeders (Fisher 1952). As fulmars do not build nests, our survey protocol relied on counts of apparently occupied sites (AOSs), a method widely used in northern fulmar monitoring (Walsh et al. 1995; Mitchell et al. 2004). AOSs correspond to sites where either direct proof of breeding is recorded (an egg or chick) or a bird is observed in a brooding position at least once during the breeding period. Each year, colonies were visited an average of six times during the breeding period. It should be noted that every site where chicks were observed, even outside the focus period (19 May–31 July), was considered to be an AOS. Seventy-four AOSs were monitored at Beg, 89 at Toull, 36 at Stiff and 331 at Keller.

Estimation of colonization and extinction rates, proportion of breeders among adults, and population growth rate

We used the robust design spatial occupancy model (MacKenzie et al. 2003) implemented in the program PRESENCE (Hines 2006). This model allows the user to estimate the probability of site occupancy as well as site colonization and extinction rates when a species is detected imperfectly. The model allows assessment of changes in site occupancy states between T primary sampling periods (in the present study, nine annual periods from 1997 to 2005). Within each primary period, we attempted to detect fulmars in AOSs in k_i surveys (on average, six surveys per

primary period). This approach is akin to Pollock's robust design for mark–recapture studies in which k_t surveys represent secondary sampling periods within each primary period (Pollock et al. 1990; MacKenzie et al. 2003). The approach thus permits estimation of extinction and colonization rates and accounts for detection probability. The extinction rate is defined as follows: if a site is occupied in year t , it can either go 'extinct' with probability ε in year $t + 1$ or remain occupied with probability $1 - \varepsilon$. The colonization rate is defined as follows: if a site is not occupied in a year t , it can be colonized with probability γ in year $t + 1$ or remain unoccupied with probability $1 - \gamma$. This model also allows computation of some derived estimates such as the occupancy-based population growth rate ($\lambda_{\text{occupancy}}$), which is calculated as the ratios of successive occupancy estimates (Hines 2006). The individual survival rate was obtained from published studies based on capture–recapture analyses of other populations (details are provided in the results and discussion) and was compared to our data using a capture–recapture approach based on Pradel's model (1996) and applied to site persistence; further details on this approach are presented in Appendix S2 in ESM. Finally, we estimated the proportion of breeders among adults (B) (and thus $1 - B$ was the proportion of sabbatical birds) by combining estimates obtained for the nest extinction rate and individual adult survival (detailed computations are presented in Appendix S3 in ESM).

Another issue to consider is potential heterogeneity in site quality within a given colony. Such heterogeneity may result in differences in attractiveness among sites and thus bias parameter estimations.

Estimation of reproductive success

The reproductive success (R ; R_{colony} or R_{year}) was estimated as the number of chicks considered as fledging in a given year divided by the number of AOSs estimated (*Nest*) by the robust design spatial occupancy model. Variation in reproductive success among years and colonies was investigated using a generalized linear model (GLM; with a F test in order to account for overdispersion, Faraway 2006) implemented in the R 2.10.1 statistical software (R Development Core Team 2008), specifically using the stat package.

Population dynamics analysis with matrix model

To investigate the population dynamics and to evaluate the potential role of immigration in population growth, we used a deterministic age-classified extended Leslie-matrix model. This approach allowed us to examine ergodic

population properties, such as population growth rate (λ), sensitivity of λ to various demographic components, and stable distribution of age classes (Caswell 2001). This model was implemented with the program ULM (Legendre and Clobert 1995; Ferrière et al. 1996).

First, we constructed a typical fulmar cycle life (Fig. 2) and established demographic parameters using published studies. Because northern fulmars start to breed from their sixth to their twelfth year of life (Dunnet et al. 1979), we considered that all individuals start to reproduce at 9 years of age in the main simulation model. Alternative models and results that assumed a progressive increase of recruitment of individuals between 6 and 12 years of age are presented in Appendix S4 in ESM. We assumed no senescence and no site limitation, which is consistent with observations on the study population. Survival rates assessed with capture–recapture methods are generally high (0.971: Dunnet et al. 1979; 0.969: Hatch 1987; 0.972: Balmer and Peach 1997; 0.94–0.97: Grosbois and Thompson 2005). We did not consider any differences in survival between age class owing to the lack of available information, because in long-lived birds variation in survival between age classes is weak and difficult to detect (Cam et al. 2002; Grosbois and Thompson 2005; Sandvik et al. 2005). Following the method of Hatch (1987), the proportion of breeding birds among adults was set to 0.8. On the basis of published data, northern fulmar reproductive success varies greatly through time and among regions, with an average of 0.44 (range 0.20–0.95) for colonies in the British Isles during the period from 1986 to 2002 (Mavor et al. 2004) and 0.41 in Alaska (Hatch 1987). We ran this model with the immigration rate (M) set to zero and compared outputs with the population status of published studies.

Second, the demographic parameters estimated indirectly from the robust design spatial occupancy model, such as the proportion of breeders among adults (B ; for further details see Appendix S3 in ESM), were integrated into the matrix. We also included estimates of reproductive success (R) and survival (S) obtained from the literature. We then compared the population growth rate estimated from the robust design spatial occupancy model ($\lambda_{\text{occupancy}}$) to the value of λ_{matrix} computed from the matrix model with the immigration rate M set to zero and conducted elasticity analyses.

Finally, we included in this matrix model the rate of immigration as an additional process able to explain possible differences between predicted and observed dynamics. Immigration was modeled as a rate (Fig. 2) implemented for each age class except the first class, because fulmars are considered to be highly pelagic in this period of their life (Hatch and Nettleship 1998).

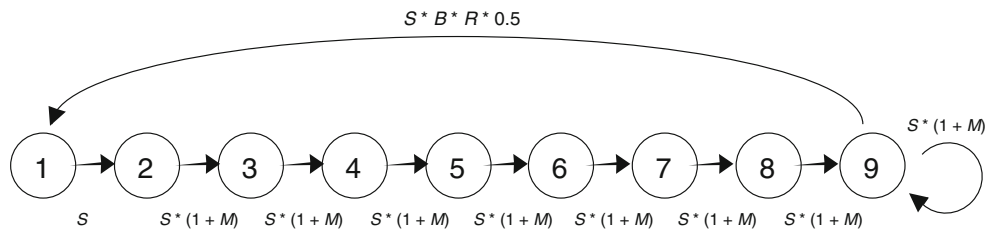


Fig. 2 Northern fulmar life cycle, where S is the survival rate, R is the reproductive success, B is the proportion of breeders, and M is the immigration rate

Table 1 Performance of different robust design spatial occupancy models, in which Ψ = occupancy, γ = colonization, ε = extinction, d = detection, t = annual trend, c = colony, i = identity and $(.)$ = a constant

Model	AIC	Δ AIC	AIC weight	Np
$\Psi(c), \gamma(c + t), \varepsilon(c + t), d(c + i)$	14332.54	0.00	0.998	72
$\Psi(c), \gamma(c), \varepsilon(c), d(c + i)$	14344.75	12.21	0.002	70
$\Psi(c), \gamma(.), \varepsilon(.), d(i)$	14354.02	21.48	0.000	60
$\Psi(c), \gamma(c + t), \varepsilon(c + t), d(c)$	14456.25	123.71	0.000	18
$\Psi(c), \gamma(c + t), \varepsilon(c), d(c)$	14456.74	124.20	0.000	17
$\Psi(c), \gamma(c + t), \varepsilon(c + t), d(.)$	14458.73	126.19	0.000	15
$\Psi(c), \gamma(c + t), \varepsilon(c), d()$	14459.11	126.57	0.000	14
$\Psi(.), \gamma(c + t), \varepsilon(c), d(c)$	14464.28	131.74	0.000	14
$\Psi(c), \gamma(c), \varepsilon(c), d(c)$	14472.20	139.66	0.000	16
$\Psi(c), \gamma(c), \varepsilon(c + t), d(c)$	14472.45	139.91	0.000	17
$\Psi(c), \gamma(c), \varepsilon(c), d(.)$	14474.14	141.60	0.000	13
$\Psi(c), \gamma(c), \varepsilon(.), d(c)$	14474.28	141.74	0.000	13
$\Psi(c), \gamma(c + t), \varepsilon(c + t), d(.)$	14485.87	153.33	0.000	4
$\Psi(.), \gamma(.), \varepsilon(.), d(.)$	14485.87	153.33	0.000	4
$\Psi(c), \gamma(t), \varepsilon(c), d(c)$	14899.01	566.47	0.000	13
$\Psi(c), \gamma(t), \varepsilon(.), d(c)$	14901.45	568.91	0.000	10

For each model, we provide the number of parameters (Np), the Akaike information criterion (AIC) value, the difference in AIC value from the previous model (Δ AIC), and the AIC weight. When more than one variable was tested for a given parameter, we tested models with only additive effects between variables (+)

Results

Estimation of colonization and extinction rates, proportion of breeders among adults, and population growth rate

The best model (selected on the basis of the Akaike information criterion; AIC) assumed that the occupancy, colonization, extinction and detection rates all vary among colonies (Table 1). In addition, the colonization and extinction rates both showed a temporal trend. The detection probability of occupied nests varied across sessions and across colonies (range 0.44–0.53; average value weighted by colony size 0.49 ± 0.02). Thus, with six visits per reproductive season, the overall annual detection probability is 98% ($1 - (1 - 0.49)^6$).

The extinction rate was estimated to be 0.356 ± 0.007 (Beg: 0.261 ± 0.001 ; Keller: 0.359 ± 0.001 ; Stiff: 0.400 ± 0.001 ; Toull: 0.406 ± 0.003), thus the AOS persistence in consecutive years was about 64%. The colonization rate was estimated to be 0.143 ± 0.005 (Beg: 0.158 ± 0.016 ; Keller: 0.136 ± 0.007 ; Stiff: 0.209 ± 0.027 ; Toull: 0.131 ± 0.014).

Our computations of the proportion of breeders among adults suggested that B was between 0.64 and 0.76 (average 0.684 ± 0.027 ; for further details see Appendix S3 in ESM).

The estimated population growth rates varied between colonies (Beg: 1.123 ± 0.013 ; Keller: 1.036 ± 0.055 ; Stiff: 0.978 ± 0.167 ; Toull: 1.060 ± 0.106). Weighting these growth rates by the colony size observed in the first year of the study led to an average growth rate of 1.049 for

Ouessant. This further led to a global increase by a factor of 1.5 over the study period, which was consistent with the field census.

Reproductive success

The reproductive success (i.e., the average number of fledged offspring per AOS, where the number of AOS was the number of nests estimated with the robust design spatial occupancy model) was estimated to be 0.207 ± 0.0027 (Table 2). After adjustment for differences among years, no variation between colonies was detected ($F_{3,31} = 0.625$, $P = 0.605$). After adjustment for differences among colonies, no significant variation among years was detected ($F_{8,24} = 2.172$, $P = 0.068$). Over the study period, no particular trend (increase or decrease) in reproductive success was detected ($F_{1,31} = 0.754$, $P = 0.39$).

Population dynamics analysis

The matrix model implemented with published demographic parameters ($R = 0.41$ to 0.44 ; $B = 0.8$ to 1 ; $S = 0.97$) provided a range of population growth rates from $\lambda = 0.96$ to

$\lambda = 1.07$, which was consistent with the demographic trends of most North European populations of fulmar (Dunnet et al. 1979; Hatch 1987; Balmer and Peach 1997; Mavor et al. 2004). However, when implemented with demographic parameters estimated from our data ($R = 0.207$; $B = 0.684$; $S = 0.957$; see Appendix S2 in ESM for details on survival estimation) and with an immigration rate set to zero, the matrix model yielded $\lambda = 0.84$. Such a growth rate would result in a drastic decrease in the population, which is not consistent with the actual population dynamics.

The sensitivity of growth rate to S was high, whereas variation in R and B had weaker effects on λ (Table 3). However, on the basis of the actual variations in demographic parameters (i.e., the difference between Ouessant estimates and the maximum recorded values of the parameters), reproductive success appeared to be the factor with the most impact on population dynamics (Table 3). Another property of age-classified models is the stable age distribution. At demographic equilibrium, adults (9 years old and older) were predicted to comprise 55% of the fulmar population.

To examine how parameterizations (S , B , and R) could have biased growth rate estimates or if some level of

Table 2 Reproductive success of northern fulmars at four colonies on Ouessant from 1997 to 2005

Year	Beg	Keller	Stiff	Toull	Total
1997	0.104	0.256	0.162	0.000	0.193 ± 0.054
1998	0.295	0.133	0.248	0.200	0.169 ± 0.035
1999	0.237	0.107	0.166	0.171	0.134 ± 0.027
2000	0.118	0.109	0.083	0.129	0.111 ± 0.009
2001	0.377	0.042	0.251	0.389	0.163 ± 0.080
2002	0.253	0.347	0.418	0.333	0.335 ± 0.034
2003	0.095	0.284	0.586	0.296	0.257 ± 0.101
2004	0.109	0.264	0.084	0.217	0.202 ± 0.043
2005	0.145	0.000	0.251	0.190	0.088 ± 0.053
Total	0.193 ± 0.034	0.171 ± 0.040	0.250 ± 0.054	0.214 ± 0.039	0.207 ± 0.027

Table 3 Sensitivity of population growth rate (λ) to survival (S), reproductive success (R), the proportion of breeding individuals (B) and the migration rate (M)

Parameter	Ouessant estimate	Maximum value recorded	α (%)	E_x	αE_x (%)
S	0.957	0.97 ^a	1	1	1
R	0.207	0.95 ^b	359	0.053	19
B	0.684	0.80 ^c	17	0.577	9
M	0.16–0.27	–	–	0.028	–

E_x is the elasticity of λ to each demographic parameter. α is the percentage of variation between the Ouessant estimate and the maximum recorded value for each parameter. αE_x quantifies the importance of each parameter on λ according to elasticity and to the actual level of variation of the parameter

^a Dunnet et al. (1979) and Balmer and Peach (1997)

^b Mavor et al. (2004)

^c Hatch (1987)

immigration (M) is necessary to explain actual population dynamics, we computed various combinations of parameters (S , B , R , and M) that were consistent with the robust design spatial occupancy model estimate of population growth ($\lambda = 1.049$; Fig. 3). The results indicated that when the observed values of S , B and R were considered, a high annual rate of immigration was necessary ($M = 0.269$; Fig. 3) to yield $\lambda = 1.049$, or a very high and simultaneous increase in all parameters (S , B , and R) was necessary to obtain $\lambda = 1.049$ in the absence of immigration.

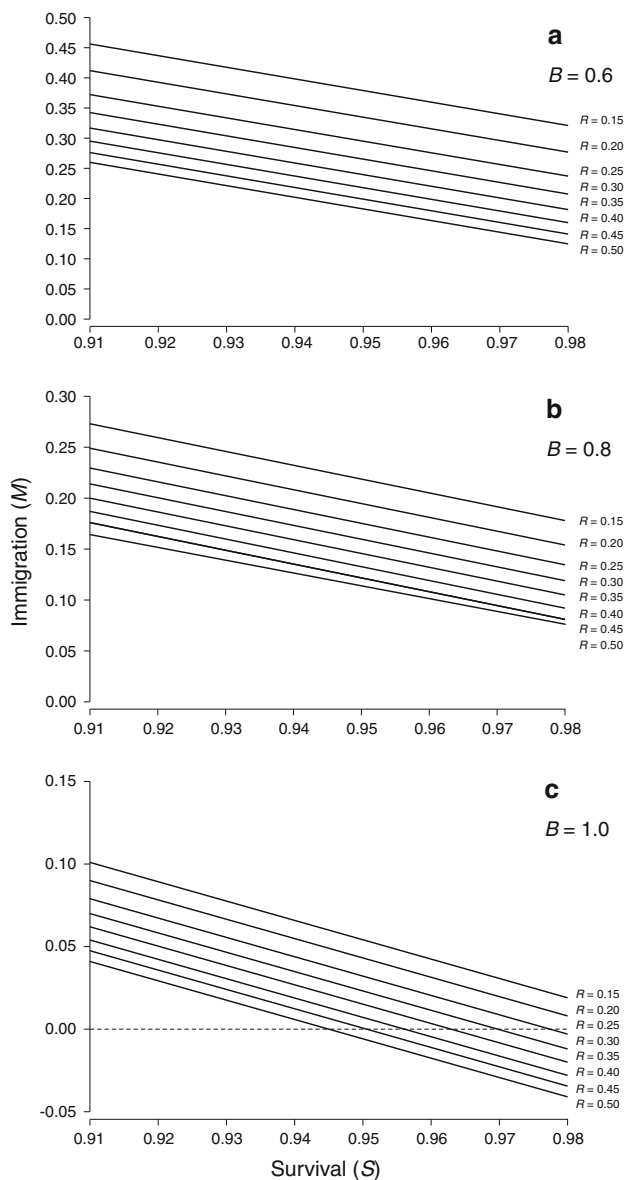


Fig. 3 Relationship between survival rate (S), immigration rate (M) and reproductive success (R) for a fixed annual growth rate of 1.049 and a fixed proportion of breeding birds (B) of 0.6 (a), 0.8 (b) and 1.0 (c). Note differences among panels in the y-axis scale

Discussion

We investigated the processes underlying the population dynamics of the northern fulmar, a long-lived seabird, in the southern limits of its distribution range. We used a robust design spatial occupancy modeling approach, which is considered to be an efficient statistical method to account for detection probability in the estimation of parameters of biological interest. The model was applied to data derived from an AOS survey of four colonies on Ouessant Island. We obtained evidence that, despite their strong size increase, the populations likely functioned as a sink, i.e., natural recruitment alone did not explain the observed growth rate. This result provides useful information for the managers of this protected area in the context of global changes and the need for the optimization of conservation management.

The strong disagreement between the robust design spatial occupancy model estimate of population growth ($\lambda = 1.049$) and the growth rate computed from the matrix model in the absence of immigration ($\lambda = 0.84$) may be a result of: (1) incorrect assumptions with regard to site and mate fidelity and/or the lack of site reuse following site abandonment; (2) underestimation of demographic parameters; and (3) occurrence of immigration in Ouessant colonies. These alternatives are discussed below.

Release of working hypotheses

The high fidelity of long-lived seabirds to their site and partner is well documented (Greenwood and Harvey 1982; Boulinier and Danchin 1996), particularly in the case of the northern fulmar (Dunnet et al. 1963). However, the assumption that sites are not reused by other breeding birds when previous breeders have died may not be robust and may bias survival estimation. In situations in which sites are reused by other breeding birds, we thus attempted to overestimate bird survival, which also did not seem appropriate. Such biases should have a low impact on parameter estimation, particularly in growing populations where no site saturation seems to occur, as was the case in our study site: currently less than 25% of favorable cliffs are occupied on Ouessant (C. Kerbiriou, unpublished data).

Biases in parameter estimation

Strong and consistent biases in R , B and S parameters are unlikely because our estimates are generally consistent with published estimates. First, if some AOSs are occupied by non-adult birds, R may be underestimated. Hatch (1987) and Falk and Møller (1997) estimated that the proportion of sites occupied by non-breeders, such as young birds, was 21.8 and 21.4%, respectively. Given these proportions, a

more realistic reproductive success value could be 0.265 (i.e., $0.207/(1 - 0.22)$). An alternative (extreme) scenario would be to assume that all non-adult, non-juvenile birds (i.e., birds from 2 to 8 years of age) occupy sites. According to the age distribution at demographic equilibrium, this would yield a maximum value of 43% of non-breeding birds occupying sites. In this case, R could reach 0.361 (i.e., $0.207/(1 - 0.43)$).

Secondly, the estimate of survival rate through AOS persistence (see detailed computations presented in Appendix S3 in ESM) is very close to survival rates assessed by capture–recapture in other fulmar populations (0.971: Dunnet et al. 1979; 0.969: Hatch 1987; 0.972: Balmer and Peach 1997; 0.94–0.97: Grosbois and Thompson 2005) or in closely related species (0.923 in the Antarctic fulmar; Jenouvrier et al. 2005). These estimates correspond to adult survival only. Because survival rates of juvenile and immature birds are expected to be lower than adult survival rates, it is reasonable to expect an average survival rate that is lower than the adult survival rate. Given an adult survival rate of 0.97 and an immature survival rate of 0.88 (the estimate obtained for birds aged from 1 to 9 years; Dunnet et al. 1979), the average survival would then be 0.95, a value very similar to the rate estimated for Ouessant. Therefore, our survival estimates are close to previous estimates and are in agreement with the theoretical expectation that adult survival rates should exhibit low variance among populations of long-lived species (Caswell 2000; Saether and Bakke 2000).

Importance of immigration on Ouessant population dynamics

Given that the reproductive success could be re-estimated from 0.21 to 0.27 or even 0.36, the proportion of non-breeders could be lower than published estimates (0.6–0.8), and that an increase in survival rates is not realistic, estimations with the matrix model were not consistent with observed growth rates unless a substantial immigration rate is considered (Fig. 3). The annual migration rate is most likely to be 0.16 (which corresponds to re-estimated parameters ($R = 0.27$, $B = 0.8$, and $S = 0.96$)). Even the most optimistic set of parameters ($R = 0.36$, $B = 1$, and $S = 0.96$) predicted an immigration rate of 0.005 to reach the observed growth rate ($\lambda = 1.049$).

In agreement with previous studies (Ollason and Dunnet 1983; Ainley et al. 1990; Cairns 1992; Inchausti and Weimerskirch 2002), our results suggest that immigration plays an important role in some local seabird population dynamics. The recruitment of migrants native to nearby populations, such as the large populations in the British Isles, is then very likely. Interestingly, whereas immigrants are expected to select the most suitable place to breed, the

observed immigration process takes place into a population with a very low reproductive success (0.21; extreme 0.09–0.34), compared to that of other areas [R average 0.44 (extreme 0.20–0.95) in the British Isles colonies during the period from 1986 to 2002, Mavor et al. 2004; R average 0.41 in Alaska, Hatch 1987]. Numerous studies have demonstrated that species use the reproductive success of conspecifics to assess the quality of different patches in a given year (Boulinier and Danchin 1997; Danchin et al. 1998). The low reproductive success observed at Ouessant could be linked to the age of migrants, if migrants are mainly young and sexually naive birds (although we did not detect any increasing trend in R , which could have reflected the ageing process of colonies). Alternatively, the low reproductive success could reflect low local food availability, which is an important factor that influences local population dynamics (Cairns 1992; Oro et al. 2003). It could also be explained by a low resilience of chicks that are localized to their peripheral thermal range.

Persistence of the Ouessant population in the Atlantic context

In the context of decreased immigration from nearby populations, the Ouessant population would be predicted to be rapidly decreasing ($\lambda = 0.84$ and 0.91 for the most realistic scenarios). Importantly, a scenario of decreased or halted immigration appears to be realistic according to the dynamics of nearby populations. Seabird censuses in the British Isles (Mavor et al. 2004) have indicated a stabilization of fulmar population sizes. In addition, Grosbois and Thompson (2005) found a significant decreasing trend in fulmar survival linked to climatic variation (the North Atlantic Oscillation). During the study period, we did not detect any particular trend in reproductive success or intrinsic growth rate on Ouessant, whereas the growth rates of other French colonies are decreasing on the basis of 1970, 1979, 1988 and 1998 surveys (among these three decades, values of λ were 1.13 ± 0.03 , 1.10 ± 0.03 and 1.05 ± 0.02 , respectively; Cadiou and Lang 2004). Thus, although the Ouessant population of northern fulmars is large and apparently increasing, it is likely to be a sink population.

Conclusion

In the context of global changes, many species currently are experiencing either range expansion (e.g., invasive species), range contraction (e.g., native species in disturbed habitats; Thomas et al. 2006), or exhibiting a shift in their range (e.g., species faced with global warming; Parmesan 1996). Therefore, greater effort should be made to

understand such processes rather than to deal with equilibrium processes. In general, marginal populations are more sensitive to environmental changes than populations located at the center of the species' range. Because of the close linkage between populations within the species' range, conservation and management of both central and marginal populations are equally important (Furrow and Amrijo-Prewitt 1995; Lesica and Allendorf 1995; Lomolino and Channell 1995; Guo et al. 2005). However, for prediction of the retraction or expansion of a species' range, monitoring boundary conditions and/or marginal populations is more effective and informative.

Survey methods, such as those developed in our study, allow easy and cost-effective monitoring of numerous populations and thus to survey trends from the boundary to the center of a species' distribution range. These methods are complementary to traditional individual mark–recapture surveys and are an efficient tool to address the demographic status of seabird populations (Gaston et al. 2009), and thus provide relevant information to managers for the hierarchization of conservation priorities.

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