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Are edge bird populations doomed to extinction? A retrospective analysis of the common guillemot collapse in Iberia

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ABSTRACT

In the first half of the XXth century, the common guillemot (*Uria aalge*) was the seabird with the largest breeding population in Atlantic Iberia (ca. 20,000 individuals), the low-latitude limit of the species breeding range. However, this population suffered a dramatic decline and is quasi-extinct at present. The decline was believed to be associated with reduced availability of pelagic prey fish due to climate change. In this study, we analyzed the population change of Iberian guillemots in the second half of the XXth century by means of a retrospective analysis. Our study showed that between 1960 and 1974 the guillemots in Iberia suffered a dramatic population crash (33.3% annual decline) and that subsequently, the population continued to decline at a slower annual rate (13.4%). Simulation models indicated that the factors driving the population crash should be related to adult survival, rather than reproduction. The analysis of environmental and fishery data suggested good climate conditions and higher or sustained availability of pelagic prey fish when the Iberian guillemots crashed. In contrast, relevant human-related factors were affecting adult mortality in that period, specially a rapid and large increase in the number of synthetic fishing nets. During the collapse, no conservation measures were undertaken to mitigate anthropogenic threats and it was assumed, in some extent, that this low-latitude edge population was somehow prone to extinction as a consequence of climate change. This study highlights that to carelessly attribute the decline of rear edge populations to climate change could be highly misleading if the population is suffering from other, particularly human, threats.

1. Introduction

Evidence suggests that modern climate change is changing the geographic distributions of plant and animal species world-wide (Parmesan and Yohe, 2003). Thus, for example, the distribution range of animal species from the Northern Hemisphere has been shifting northwards in the last 30 years (e.g. Thomas and Lennon, 1999; Walther et al., 2002). These northward shifts in the distribution of Boreal/Polar animal species are often detected by a northern margin expansion or net extinctions of the populations at the southern boundary of the species range (Thomas and Lennon, 1999; Parmesan et al., 1999). In this context, the dynamics of edge, low-latitude populations are likely to be crucial in determining species responses to expected trends in climate change (e.g. Thomas et al., 2004; Travis and Dytham, 2004). In many cases, climate change exacerbates other direct threats derived from human activities, including habitat destruction, which is

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responsible for the majority of extinctions of many animal edge and non-edge populations (Wilcove et al., 1998; Novacek and Cleland, 2001). Low-conservation concern has been promoted on populations at the southern limit (Hampe and Petit, 2005), probably because it is believed that they are intrinsically more prone to extinction (e.g. Hengeveld, 1994; Channel and Lomolino, 2000) and some climatic models are predicting their complete disappearance (Thomas et al., 2004). Contrasting with this view, it has recently been suggested that low-latitude margins are critically important for the long-term conservation of genetic diversity, phylogenetic history and evolutionary potential of species (Hampe and Petit, 2005).

In the marine environment, the majority of recent extinctions (neoextinctions) corresponds to seabirds; for example, in the North Atlantic the only extinction of a marine organism recorded in historical time was the Great Auk (*Alca impennis*) a flightless alcid (Carlton et al., 2004). Compared to other organisms seabirds are extinction-prone (Şekercioğlu et al., 2004), probably because they are located towards the slow end (i.e.: low reproductive rate) of the slow–fast continuum of life history variation (Saether and Bakke, 2000) and because low-fecundity predisposes their populations to take longer to recover if an external force causes a rapid increase in mortality rates (Bennett and Owens, 1997). In fact, many seabird populations are threatened by human-induced mortality caused by oil spills, by-catch mortality and shooting (e.g. Gales et al., 1998; Tasker et al., 2000; Wiese et al., 2004; Votier et al., 2005). There is a body of evidence that large scale environmental conditions influence reproductive success of seabirds (e.g. Aebischer and Coulson, 1990; Murphy et al., 1991); however, the population dynamics of these long-lived species are more sensitive to variation in adult survival (Croxall and Rothery, 1991; Russell, 1999). Recent studies with large data sets indicate that environmental factors especially during catastrophic events (e.g. climatic and oceanographic anomalies) also influence the adult survival rates of seabirds (Jones et al., 2002; Frederiksen et al., 2004; Sandvik et al., 2005), with additive effects to the mortality attributable to human activity (e.g. oil pollution, Votier et al., 2005). As far as we know, no studies have analysed recent extinctions of seabird populations in the limit of their distribution range. Here, we use population data, population matrix models (Caswell, 2001) and temporal data of environmental factors and human activities to investigate the quasi-extinction of the common guillemot (*Uria aalge*) in Iberia, the southernmost limit of the species in the Atlantic.

The common guillemot is a diving seabird with a boreal circumpolar distribution and a total breeding population over 7 million pairs (Harris and Wanless, 2004). Historically, the populations breeding at the Atlantic Coast of the Iberian Peninsula marked the low-latitude limit of the species breeding range. This distribution pattern has been related with the geographic extent of boreal water masses and associated biota and therefore the Iberian breeding area was considered as a relict population (Nettleship and Evans, 1985). Fifty years ago, the common guillemot was probably the seabird with the largest breeding population in Atlantic Iberia, (ca. 20,000 individuals; Bárcena et al., 1984). However, the population suffered a dramatic decrease in the second half of the 20th century and is quasi-extinct at present (as far as we know, no breeding attempts have been recorded since 2003). The extinction of the Iberian population will result in a very large reduction of the latitudinal range of the species (ca. 10 lat. degrees), a distribution range reduction unparalleled in the North Atlantic.

Although the species was listed as "critically endangered" in Spain and Portugal (Blanco and González, 1992; ICN, 2006; Mouriño et al., 2004) no conservation measures or action plans have been undertaken. The little concern caused by the extirpation of common guillemots from Atlantic Iberia was probably due to the belief that this southernmost population was intrinsically prone to extinction under natural conditions. Thus, early analyses (at least since 1989; see Programa Arao, 1991; Blanco and González, 1992) assumed that reduced availability of pelagic prey fish due to climate change was the primary factor driving the population into extinction. Nevertheless, other threats, including anthropogenic factors were operating during the Iberian guillemot collapse (Bárcena et al., 1984). The aim of this study was to document and analyze the population change of Iberian guillemots by means of a retrospective analysis. First, we analysed the changes in population size, trying to identify whether the decline was constant or, alternatively, whether there was a period with a more drastic decline. Afterwards, we made a retrospective analysis using a population modelling approach. In the absence of data on Iberian guillemots, we reviewed the literature to develop a stage-classified model using average population parameters and their variability. Consequently, this retrospective diagnosis is inherently comparative and seeks why Iberian population disappeared in comparison with other "healthy" populations (Caswell, 2001). By running the models while holding different demographic parameters constant in turn, it is possible to investigate which stage of the lifecycle has probably been affected sufficiently to have driven the population trends. Lastly, we analysed how different threats (human and environmental) changed through time and whether the changes observed were in accordance with the history of the guillemot extinction in Iberia.

2. Methods

2.1. Population trends

Historically, guillemots bred in 10 localities dispersed across the Atlantic coast of the Iberian Peninsula, seven of them with available data about population changes (Fig. 1), including counts (individuals or pairs) and estimations made by different teams (e.g. Bernis, 1948; Lockley, 1952; Bermejo and Rodríguez Silvar, 1983; Bárcena, 1985; Bárcena et al., 1987; Programa Arao, 1991; Mouriño et al., 2004; Plano Sectorial Rede Natura 2000, 2006). For comparative purposes, counts of individuals were multiplied by 0.67 to estimate the number of breeding pairs (Harris, 1989); this is a correction factor generally applicable in Britain. In each colony, the instantaneous growth rate per period with two population estimates was calculated as $r = (\ln N_t - \ln N_0)/t$, where N_0 is the population size at the outset, t is the time in years, N_t is the population size after time t and r is the instantaneous growth rate of the population. The annual multiplication rate (λ) was estimated as $\lambda = e^r$ and the annual growth rate (%) was expressed as $(\lambda - 1) \cdot 100$.

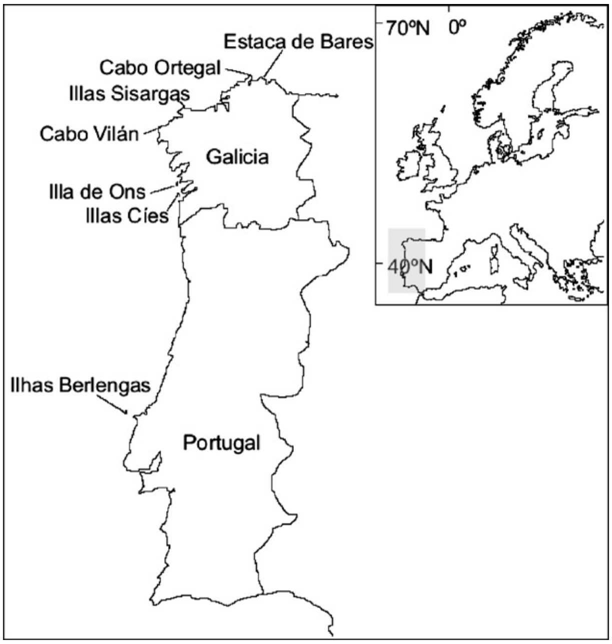

Fig. 1 – Geographical distribution of the main common guillemot (*Uria aalge*) breeding colonies in the Iberian Peninsula ca. 1950.

Table 1 – Model input population parameters for the common guillemot (Uria aalge) and their reported ranges (based on literature data)

Parameter	Mean	SD	Range
s_0, juvenile survival[a]	0.342	0.563	0.21–0.41
s_a, adult survival[b]	0.914	0.051	0.74–1.00
r_5, recruitment of 5-year old birds[c]	0.084	0.070	
r_6, recruitment of birds older than 6 years[c]	0.310	0.090	
f_a, fertility of experienced adults[d]	0.651	0.200	0.07–0.97

a Birkhead and Hudson, 1977; Hatchwell, 1988, Hedgren, 1980; Murphy et al., 1986; Lindner, 2000.

b Birkhead and Hudson, 1977; Birkhead and Nettleship, 1985; Hedgren, 1980; Murphy et al., 1986; Burger and Piatt, 1990; del-Nevo, 1990; Harris and Wanless, 1988; Hatchwell, 1988, 1991; Harris, 1991; Sydeman, 1993; Harris et al., 1994; Harris and Wanless, 1995; Harris et al., 2000; Lindner, 2000; Ainley et al., 2002.

c Lindner, 2000.

d Birkhead, 1977; Hedgren, 1980; Hunt et al., 1986; Nettleship and Birkhead, 1985; Birkhead and Nettleship, 1987; Hatchwell, 1988; Harris and Wanless, 1988, 1989, 1990; Burger and Piatt, 1990; del-Nevo, 1990; Harris et al., 1992; Monaghan et al., 1992, 1996; Murphy and Schauer, 1994; Parrish, 1995; Murphy and Schauer, 1996; Piatt and Anderson, 1996; Bryant et al., 1999; Heubeck, 1999; Regehr and Rodway, 1999; Parrish et al., 2001; Ainley et al., 2002; Öesterblom and Olsson, 2002; Davoren and Montevecchi, 2003.

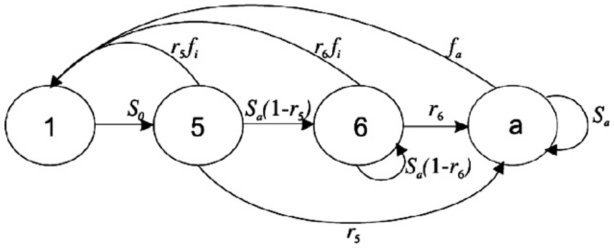

Fig. 2 – A life cycle diagram for the common guillemot (*Uria aalge*). Stage 1 is juvenile birds of age one, stage 5 is immature birds of age five, stage 6 is immature birds of age six or more and stage *a* corresponds to adult breeders. Transition probabilities (arrows) among stages: S_0 is survival for juvenile birds to age four, S_a is survival for adult birds (older than five); r_5 is the proportion of recruits of age five, r_6 is the proportion of recruits of age six or older; f_i is the fertility of first time breeders, and f_a is the fertility of experienced breeders.

2.2. *Population modelling*

Retrospective diagnoses of population decline at Iberia were assessed by population modelling. The final objective of the modelling was to determine which combination of population parameters could explain the observed population dynamics. In the absence of data for Iberian guillemots and since diagnosis is inherently comparative (Caswell, 2001), we first developed a stage-classified model using population parameters and their variance in other localities, derived from the literature (Table 1). We modelled the life-cycle of the population based on its life-history traits using seven stage classes: 1-year old juveniles, 2-year old immatures, 3-year old immatures, 4-year old immatures, 5-year old immatures, immatures older than 6 years and breeding adults. In the common guillemot the period of immaturity is long (5 years), with individuals remaining unobservable at sea; thus for modelling purposes, we assumed that all mortality between fledging and the fifth year happens during the transition from the fourth to the fifth stage (Lindner, 2000); thus, juvenile birds survive to stage 5 with probability s_0 (Fig. 2). The remaining population parameters were: s_a, adult survival; r_5, recruitment of 5-year old birds; r_6, recruitment of birds older than 6 years; f_i, fertility (reproductive success) of first time breeders; f_a, fertility of experienced adults. Fertility of first time breeders was considered a fraction (0.6) of the fertility of experienced adults (according with data from Stora Karlsö, Sweden [Hedgren, 1980] and Skomer, Wales [Lindner, 2000]). A balanced sex-ratio was assumed in the models (Parker et al., 1991). Probabilistic distributions of demographic parameters were applied to add demographic stochasticity, which assigned population sizes to integer values. For environmental stochasticity, each demographic parameter was randomly selected from a normal distribution generated from average and variance estimates obtained from literature sources (Table 1). We used a CSIRO program called PopTools (an add-in to Excel, Greg Hood, http://www.cse.csiro.au/poptools/) to perform projection analysis.

Starting population age structure was set to a stable age distribution, based on values derived from running the baseline model (with the average population parameters) until population growth and age structure stabilised. Then, we analysed the asymptotic population multiplication rate of the baseline model, obtained as the largest eigenvalue of the matrix, denoted as λ, and its sensitivity to changes in population parameters. Moreover, we analysed the influence of initial population size and demographic stochasticity on extinction probability by running Monte Carlo simulations (1000 runs) over time (50 years) with different initial population size; extinction probability was calculated as the proportion of simulations where the population was extinct.

In order to analyse whether changes in a demographic parameter can or cannot account for the population trends observed in each period, colonies with available data were simulated by Monte Carlo analysis (1000 runs) under one baseline and three extreme-case scenarios (varying only a population parameter from the baseline model): (1) with no reproduction, thus assuming that no chicks were produced (2) with the lowest survival recorded (0.74, see Table 1), (3) with catastrophic mortality (0.5). We estimated the probability that simulations could explain the observed decline as the proportion of simulated trajectories with a population decline equal or higher than reported. In addition, we analysed which combinations of fecundity and survival could reproduce successfully the observed trends.

Since present population size is well below the estimated minimum viable population (20 pairs, see Section 3), management options should include the facilitation of recruitment of wintering immature birds (e.g. by means of decoys) or translocations. Simulation models were used to evaluate the minimum number of recruits needed for population viability (>90% of population persistence in 50 years) as a function of adult survival rate.

2.3. *Environmental and prey changes*

We analysed changes in the North Atlantic Oscillation (NAO) index, sea surface temperatures (SST) and fisheries landings data between 1940 and 2000. There are growing evidences that climatic oscillations such as the NAO are regulating forces on marine and terrestrial ecosystems (Ottersen et al., 2001). Winter NAO indices (http://www.cgd.ucar.edu/cas/jhurrell/indices.html) can be useful to assess winter severity over a large regional scale, with positive values indicating high winter temperatures and precipitation (Ottersen et al., 2001). Variability in the NAO index seems to influence marine fish stocks (Guisande et al., 2004) and population dynamics of common guillemots (Votier et al., 2005; Crespin et al., 2006). Thus, for example, over-winter survival of adult Skomer Island guillemots (Atlantic Iberia is one of their main wintering grounds) was negatively affected by high values of the NAO index (Votier et al., 2005). SST is believed to indicate environmental local conditions influencing the adult survival of guillemots in some regions (e.g. Barents Sea, Sandvik et al., 2005). SST data refers to the 40–44° N and 7–9° W grid and were extracted from the ICES database (http://www.ices.dk/ocean/) which started in 1950. Due to large yearly and monthly differences in sampling effort, we selected February and May SST values, the months with more data available throughout the study period, describing, respectively, winter and breeding conditions for common guillemots.

Changes in prey fish abundance were assessed by using fisheries landings records. Nothing is known about the diet of Iberian common guillemots, however, throughout its distribution range, the species feeds on a variety of shoaling pelagic fish, mainly Clupeidae and Ammodytidae (Bradstreet and Brown, 1985). We analysed available data of annual landings of the main targets of the pelagic fishery in coastal Atlantic Iberia: sardine (*Sardina pilchardus*), horse mackerel (*Trachurus* spp.), anchovy (*Engraulis enchrasicollis*) and sprat (*Sprattus sprattus*); no data were available for sandeels (see Velando and Freire, 1999a). The studied species form large schools usually close to the coast (i.e. within range of breeding colonies) and up to about 50 m depth from the sea surface. Fishery data were obtained from various sources, including the ICES database (ICES CM, 2005) for divisions VIIIc (Cantabrian Coast to Fisterra) and IXa (Fisterra to Guadiana River, excluding the Southern Spanish Atlantic) and the Annual Reports of the Spanish Fisheries Administration, Northwest Region 1941–1987 (Dirección General de Pesca Marítima 1941–1978, 1979–1986). Similar results were achieved when prey changes at a more local scale (Port of Vigo landings records from 1940 to 1991) were analysed (data not shown).

2.4. *Mortality causes and changes in human-related factors*

Because there were no ringing recoveries of Iberian guillemots, and in order to investigate the causes of mortality, we examined the recovery circumstances of 135 wintering guillemots recovered in Spain from the database provided by the Dirección General de Conservación de la Naturaleza (Ministerio de Medio Ambiente, Spain). We did not study temporal trends because only four ringed guillemots with known recovery circumstances were recorded in the crash period (1960–1974, see Section 3).

We studied the changes in fishing nets (gillnets and driftnets) in Galicia as recorded by the Annual Reports of the Spanish Fisheries Administration, Northwest Region 1932–1967 (Subsecretaría de la Marina Civil, 1933–1935; Dirección General de Pesca Marítima 1941–1968, Annual Reports ceased to inform about fishing nets in 1967). To investigate about the change from vegetal (hemp, abaca, sisal, cotton, linen) to synthetic (nylon, vinyl, polyethylene) fibres in the fisheries of Atlantic Iberia we examined the advertisements of fishing gear included in the yearly special issue of the biweekly journal ‘Industrias Pesqueras’. This journal is edited by the Association of Ship Owners of Vigo, which is the largest fishing port in the study area.

Finally, to assess the spillage of oil in the Iberian Atlantic due to major ship wrecks, we used data of all the wrecks that occurred since 1950 as recorded by the CEDRE (Centre de Documentation, de Recherche et d’Expérimentations sur les Pollutions Accidentelles des Eaux; http://www.le-cedre.fr/). Major wrecks in the area involving the release of hazardous pollutants into the sea were also considered.

2.5. *Statistics*

We performed one-way ANOVA to test for differences between periods (before, after and during the guillemot population crash) in environmental and fishery data. Dunnet tests were used for post hoc multiple comparisons, with the crash period as control period (Zar, 1999). Correlations between variables were estimated by Pearson coefficients. Results are given as mean ± SE.

3. Results

3.1. *Population trends*

In Atlantic Iberia the common guillemot was a very common seabird and ca. 8000 breeding pairs in seven major colonies were estimated between 1940 and 1960 (Fig. 2a). The population showed a drastic decline, dropping to 185 pairs in 1981 (10–16% of average annual decline). Before 1981, three main colonies (Estaca de Bares, Cabo Ortegal, Illa de Ons) were extinct, whereas the Illas Cíes colony disappeared in 1988. The remaining colonies (Illas Sisargas, Cabo Vilán and Ilhas Berlengas) continued to decline in the following years and only 45 pairs were estimated in 1994 (10% average annual decline). In 2003, the guillemot population was restricted to a few birds attending Ilhas Berlengas and Cabo Vilán and no breeding evidence has been recorded afterwards. The analysis of population changes by periods revealed that population changes were similar among colonies ($F_{2,8} = 2.21$, $p = 0.15$), and were not influenced by colony size ($F_{1,9} = 0.14$, $p = 0.72$). Nevertheless, there were significant differences among periods ($F_{3,10} = 3.94$, $p=0.043$; Fig. 3b); and the post hoc analysis revealed that these differences were due to the first period thus, the annual multiplication rate changed from $-33.3 \pm 4.7\%$ during 1960–1974 (thereafter crash period) to $-13.4 \pm 3.3\%$ between 1974 and 1994 (Fig. 3b).

3.2. *Population modelling*

Matrix models with average population parameters derived from the literature (see Section 2) were used to simulate the dynamics of a baseline population of common guillemots. Stochastic (demographic and environmental) simulations of this matrix predicted an asymptotic multiplication rate (λ) of 1.004 for the baseline model. Adult survival was the population parameter with higher influence on λ (Fig. 4a). Changes in initial population size with demographic stochasticity had a strong effect on extinction probability in 50 years (Fig. 4b). Below 20 pairs, the probability of extinction of a baseline population increases exponentially; however, population sizes over 30 pairs prevent the risk of extinction.

Between 1960 and 1974 only the catastrophic mortality scenario reproduced the population decline observed at the colonies (Table 2). In the following period (1974–1981) the low survival and, to some extent, the no reproduction scenarios were able to replicate the decline of Galician colonies. However, in Ilhas Berlengas, only the catastrophic mortality scenario was able to explain the decline. In the 1981–1989 and 1989–1994 periods, the low survival scenario reproduced well the declines observed in the colonies, except in those without decrease that were best replicated by using average (or even higher than average) parameters. Fig. 5 shows the contours of population decline as a function of reproductive success and adult survival obtained from the simulation models. In order to successfully reproduce the trend observed during 1960–1974, average adult survival should be reduced by more than 27%. In the following years (1974–1994), an 8–32% reduction in adult survival (depending on reproductive success) could produce the observed trends.

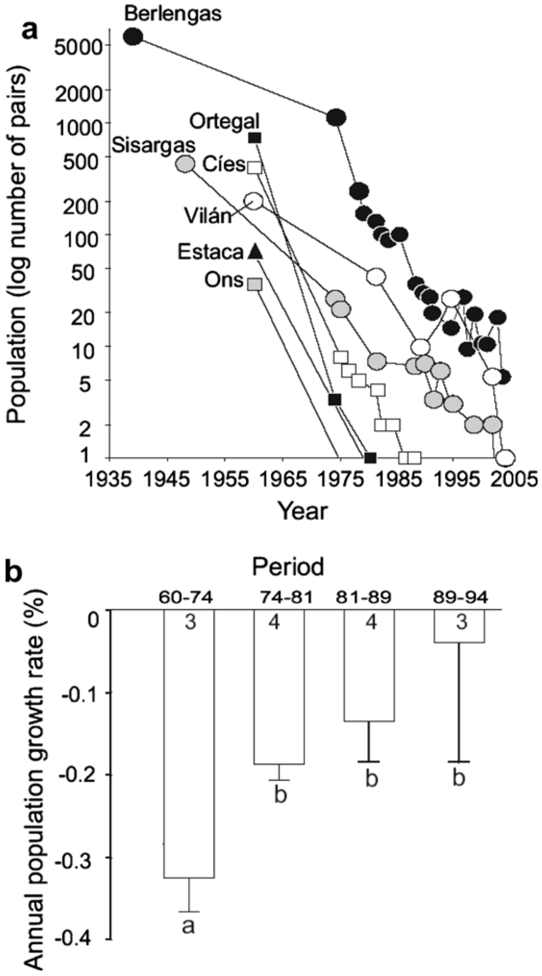

Fig. 3 – Changes in the breeding population of the common guillemot (*Uria aalge*) in the Iberian Peninsula: (a) estimations of breeding pairs at the main colonies; (b) mean ± SE annual population growth by period (for each period the number of colonies with available census data are shown at the base of the bars).

The number of recruits needed to rescue the population decreased exponentially with adult mortality (Fig. 4c). With average adult survival (0.914), 80 recruits should be enough to guarantee population persistence, but in contrast, for example, 400 recruits should be needed with an adult survival rate of 0.83.

3.3. *Environmental and prey changes*

Between 1940 and 2000, there was a trend towards a positive phase in the NAO index ($r = 0.363$; $p < 0.01$), though the trend disappeared when the variation along the complete XXth century was considered ($r = 0.058$; $p = 0.565$) (Fig. 6a). Winter NAO values varied among periods (before, crash and after; $F_{2,58} = 7.461$; $p < 0.01$). The crash period was characterized by a predominance of years with negative annual NAO values, compared to the periods before and after and the post hoc analysis indicated that differences were due to higher NAO values after the population crash ($p < 0.01$). Sea surface

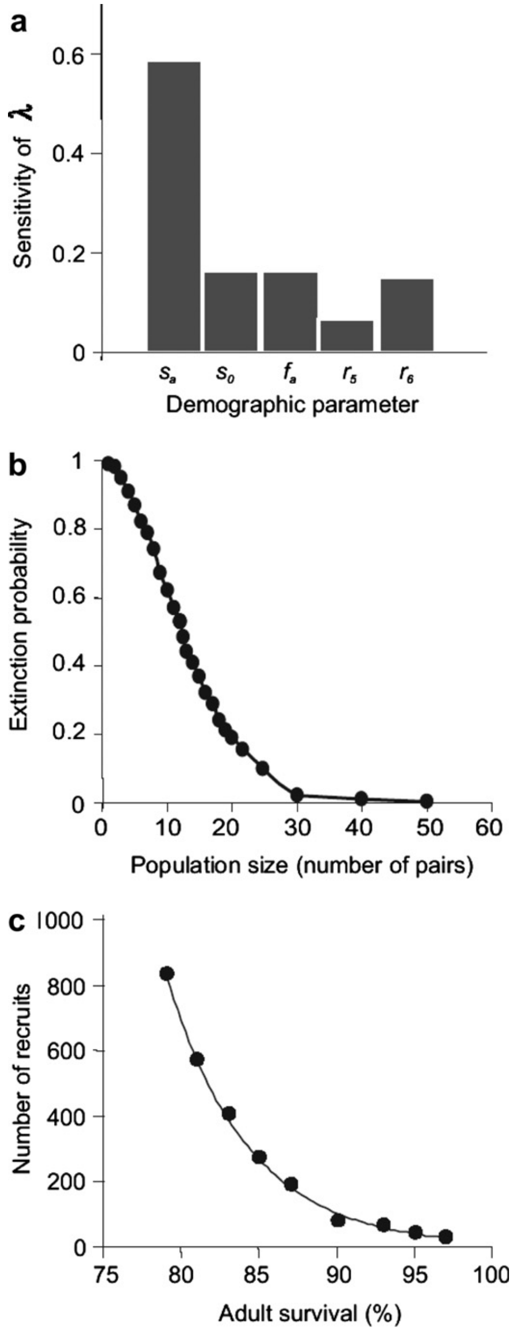

Fig. 4 – Analyses of the baseline model of a standard population of common guillemot (*Uria aalge*) with the average population parameters derived from literature (Table 1): (a) sensitivity of λ (annual multiplication rate) to changes in demographic parameters (see Fig. 2); (b) influence of initial population size on extinction probability, calculated as the proportion of simulations (1000 runs over 50 years) where the population was extinct; (c) results of simulation models used to evaluate the minimum number of recruits needed for population viability (>90% of population persistence in 50 years) as a function of the adult survival rate.

temperatures 1950–2001 showed a positive trend in February ($r = 0.550$; $p < 0.05$; $n = 16$) but not in May ($r = -0.081$; $p > 0.05$; $n = 29$). Differences in mean SST between the three periods considered were not significant (Fig. 6b; February: $F_{2,13} = 1.146$; $p > 0.05$; May: $F_{2,26} = 0.650$; $p > 0.05$).

Total pelagic fish landings (Fig. 6c) followed a positive trend in Galicia ($r = 0.684$; $p < 0.01$; $n = 35$) and no trend in Portugal ($r = 0.027$; $p = 0.836$; $n = 61$). Differences in mean landings for the three periods considered were significant for Portugal ($F_{2,58} = 24.182$; $p < 0.001$) and Galicia ($F_{2,32} = 20.518$; $p < 0.001$). In fact, mean total pelagic fish landings in Portugal peaked and were larger during the guillemot crash when compared to the periods before and after ($p > 0.001$ in both cases) and in Galicia, total pelagic fish increased along periods (before < crash < after; $p < 0.05$ and $p < 0.01$, respectively).

Sardine landings followed a negative trend in Portugal ($r = -0.265$; $p < 0.05$; $n = 61$) while no significant trends were detected in the rest of the data series (Fig. 6d). Moreover, differences in mean sardine landings between periods were not significant ($p > 0.1$ in all cases). Horse mackerel showed a continuous and marked decrease in Portuguese landings ($r = -0.887$; $p < 0.001$; $n = 39$) but not in Galicia (Fig. 6e). Mean horse mackerel landings differed among periods (Portugal $F_{1,36} = 102.3$; $p < 0.001$; Galicia: $F_{2,32} = 3.597$; $p < 0.05$). Landings during the crash period were larger than the period before in Galicia, ($p < 0.05$, no data available for Portugal) and were also larger than the following period in Portugal ($p < 0.001$) but not in Galicia ($p > 0.1$).

Anchovy and sprat landings were scarce (one or two orders of magnitude smaller than sardine and horse mackerel; Fig. 6f). Trends for anchovy landings were negative and significant for Portugal and Galicia ($r = -0.646$; $p < 0.001$; $n = 57$ and $r = -0.694$; $p < 0.001$; $N = 35$, respectively). Accordingly, differences between periods were highly significant for Portugal and Galicia ($F_{2,54} = 19.841$; $p < 0.001$; and $F_{2,32} = 10.021$; $p < 0.001$, respectively) and the *post hoc* analysis revealed that mean annual anchovy landings were smaller in the crash period compared to the period before ($p = 0.007$ and $p = 0.001$, respectively). A further reduction occurred in the period following the crash in Portugal ($p < 0.05$) but not in Galicia ($p = 0.991$). Sprat landings in Galicia (Fig. 6f) showed a positive trend ($r = 0.358$; $p = 0.035$; $n = 35$; no data available for Portugal); however, differences between periods were not significant ($F_{2,32} = 1.974$; $p = 0.155$).

3.4. *Mortality causes and changes in human-related factors*

There were four main circumstances of ring recovery between 1955 and 2000: unknown (found dead), caught in fishing nets, oiled and shot. Overall, human-induced recoveries (shot, drowned in nets and oiled) accounted for 47% of the total number of recoveries ($n = 135$). Birds caught on fishing nets were recorded during all periods and accounted for 34% of the recoveries. The first guillemot recovery from shooting was recorded in 1967 and shooting accounted for 18% of the total of recoveries in the 1960–1985 period. No guillemots were reported shot after 1984. Oiled guillemots represented a small proportion of recoveries (5%) and the first oiled guillemot was recorded in 1967. In the crash period (1960–1974), only four ringed guillemots with known recovery circumstances were recorded, one was shot, another was reported oiled and the remaining two birds drowned in fishing nets.

Table 2 – Predicted annual growth rate (mean ± SE) of Iberian common guillemot colonies in four periods (1960–74, 1974–81, 1981–89, 1989–94) under four simulated scenarios[a]

Period	Colony	Annual population growth rate (%)								
		Observed	Baseline		No reproduction		Low survival		Catastrophic mortality	
			Predicted	%S	Predicted	%S	Predicted	%S	Predicted	%S
1960–1974										
	Cíes	−26	0.2 ± 3.4	0	−4.8 ± 4.1	0	−12.7 ± 3.6	0	−30.1 ± 8.3	89.1
	Ons	−42	0.3 ± 3.6	0	−4.9 ± 4.2	0	−12.8 ± 4.5	0	−36.7 ± 9.6	40.1
	Ortegal	−32	0.5 ± 3.5	0	−5.0 ± 4.2	0	−12.7 ± 3.6	0	−29.0 ± 6.6	26.4
1974–1981										
	Berlengas	−26	0.2 ± 3.6	0	−4.5 ± 4.3	0	−13.53 ± 3.5	0	−29.3 ± 3.4	78.8
	Cíes	−15	−0.4 ± 7.5	4.4	−5.8 ± 6.2	10.1	−18.9 ± 19.8	45.2	−49.4 ± 29.3	84.6
	Sisargas	−16	−0.1 ± 4.9	2.0	−4.5 ± 5.2	1.0	−14.4 ± 6.5	25.5	−35.4 ± 17.2	97.5
	Ortegal	−18	−2.8 ± 16.3	3.5	−8.5 ± 18.9	8.2	−37.5 ± 29.2	47.8	−60.8 ± 18.4	87.6
1981–1989										
	Berlengas	−17	0.3 ± 3.9	0	−4.8 ± 4.6	1.1	−13.6 ± 4.02	20.5	−29.2 ± 5.3	99.9
	Cíes	−21	−1.2 ± 13.5	2.2	−4.9 ± 12.9	2.1	−27.6 ± 27.9	24.9	−57.6 ± 26.1	70.3
	Vilán	−17	0.6 ± 4.2	0	−5.1 ± 5.0	2.2	−13.9 ± 5.5	21.3	−33.0 ± 14.1	98.2
	Sisargas	0	−0.4 ± 7.9	48.0	−5.1 ± 9.3	73.4	−20.6 ± 20.0	98.7	−51.5 ± 22.5	100
1989–1994										
	Berlengas	−14	0.1 ± 5.0	1.4	−3.6 ± 5.3	4.9	−15.5 ± 6.4	63.4	−36.0 ± 11.8	100
	Vilán	23	−2.4 ± 8.1	100	−4.6 ± 8.1	100	−18.6 ± 13.4	100	−50.6 ± 26.7	100
	Sisargas	−18	0.2 ± 7.9	4.0	−2.8 ± 9.2	6.0	−19.0 ± 18.2	47.5	−50.13 ± 28.4	95.3

a (1) baseline conditions (with average population parameters obtained from the literature); (2) no reproduction (assuming that no chicks were produced); (3) low survival (assuming the lowest survival recorded in the literature, 0.74); (4) catastrophic mortality (assuming that annual adult survival was 0.5). The percentage of simulations (%S) that produce a population decline equal or higher than observed was tested by Monte Carlo analysis (1000 runs). For each period only the colonies with available census data were analyzed.

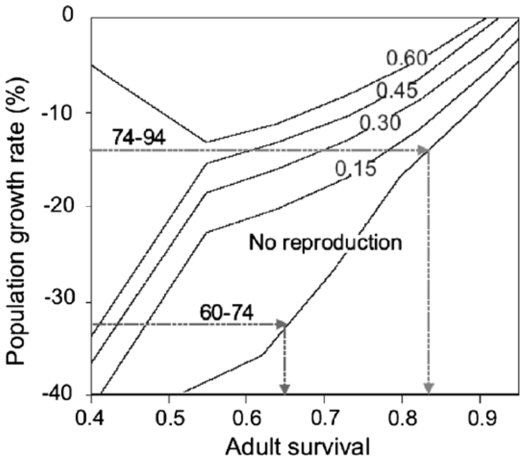

Fig. 5 – Annual multiplication rate for the common guillemot (*Uria aalge*) baseline model as a combination of adult survival and reproductive success (contour lines). Dashed lines indicate the annual multiplication rate for the main periods of decline.

The number of driftnets and gillnets in Galicia grew dramatically between 1932 and 1967 (no available data after 1967). In 1960 the number of entangling net gears was a little under 30,000 and increased sixfold to 187,296 in 1967 (Fig. 7a). According to the type of fibres advertised in the magazine “Industrias Pesqueras” the change from vegetal to synthetic fibres occurred between 1962 and 1964 (Fig. 7b). The change was swift and complete: the first add of synthetic gear (“Wercord” nylon nets) appeared in September 1962, whereas vegetal fibres had entirely disappeared from advertisements in the 1964 special issue.

Since 1950 close to half a million tonnes of oil products were spilled in the Atlantic Coast of the Iberian Peninsula as a result of 17 ship wrecks (Table 3). Three pulses (1975–1978; 1992 and 2002) involving five tankers accounted for most (89.9%) of the oil spilled. Most of the accidents occurred in winter, whereas in two occasions the wrecks occurred in the breeding period, including a wreck against Illas Cíes in May. Furthermore, two other wrecks resulted in the release of extremely hazardous substances with potential harmful effects to the marine biota including seabirds. In 1970 the vessel *Erkowitt* lost 286 tonnes of Dieldrin and in 1987 the cargo *Cason* spilled 1100 tonnes of inflammable, toxic (including aniline, diphenylmethane, *o*-cresol, dibutylphthalate) and corrosive chemicals.

4. Discussion

This study showed that between 1960 and 1974 common guillemots in Iberia suffered a population crash (33.3% annual decline), and that subsequently, the population continued to decline at a slower annual rate (13.4%) down to present near extinction. This suggests that important threats were affecting population parameters especially during 1960–1974. Results of a sensitivity analysis showed that guillemot populations are more strongly affected by adult survival than by reproductive success (see, e.g. Saether and Bakke, 2000). Indeed, simulation models indicated that bad reproduction cannot solely explain the drastic decline observed in 1960–1974.

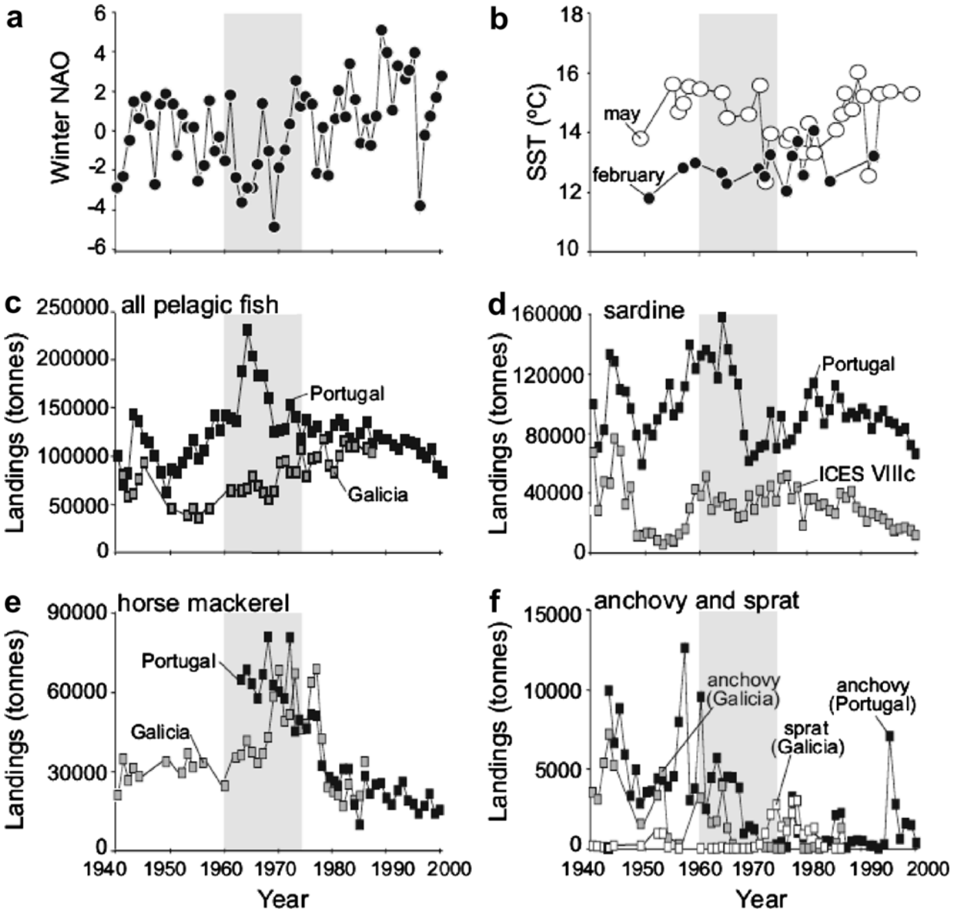

Fig. 6 – Changes in environmental parameters and pelagic fish abundance (fish landings) in Atlantic Iberia, 1940–2000. Climate data shown are: (a) the winter North Atlantic Oscillation (winter NAO) index and (b) May and February sea surface temperature (SST) in the 40° to 44° N and 7° to 9° W grid area. Annual reported fish landings are: (c) total pelagic fish landed in Portugal and Galicia, (d) sardine landed in Portugal and ICES fishery area VIIIc, (e) horse mackerel landed in Portugal and Galicia, (f) anchovy landed in Portugal and Galicia and sprat landed in Galicia. The shaded area covers the population crash period (1960–1974) for Iberian common guillemots (*Uria aalge*).

Moreover, the models indicated that adult mortality in that period should exceed average mortality by 41% to successfully reproduce the observed trend, a dramatic mortality for a long-lived seabird (see Table 1). Interestingly, simulation models also revealed that demographic stochasticity can explain the extinction of colonies below 20 pairs, as occurred in Iberian colonies after 1985. The results of simulation models should be treated with caution because they assumed that colonies were geographically closed populations (or with balanced movements). Common guillemots show a high philopatry, thus, for example, in Skomer 72% of juveniles recruited in the natal colony, although some movements were reported between colonies (Southern et al., 1965; Halley and Harris, 1993; Lindner, 2000; Parrish et al., 2001). Moreover, the assumption of no juvenile emigration is not a major weakness; even in the extreme case of complete juvenile emigration from Iberia, the conclusions are similar to no reproduction scenarios. On the other hand, adult survival in our models also includes adult emigration. Nevertheless, common guillemots show high site fidelity and rarely abandon the colony where they recruit (85–99%; Birkhead, 1977; Swann and Ramsay, 1983; Harris et al., 1996). As far as we know, no massive emigration episodes have been documented in the literature. Furthermore, nearby colonies (Brittany, Ireland and Southern Britain) did not increase their numbers (Nettleship and Birkhead, 1985; Cadiou et al., 2004; Harris and Wanless, 2004) as expected if the Iberian population had massively abandoned their breeding areas during the crash period. Although we cannot discard at all this possibility, substantial emigration seems unlikely. Thus, the factors driving population decline should specifically be related to those affecting guillemot survival.

4.1. *Changes in climate and prey availability*

We found no indication of adverse environmental conditions in the crash period. A recent work showed that high winter NAO values are associated with low survival of adult guillemots wintering in Iberia (Votier et al., 2005), whereas high SST has also been associated with low survival of Norwegian guillemots (Sandvik et al., 2005). Much on the contrary, the crash period was characterized by a NAO negative phase and low SST values, thus suggesting good environmental conditions for Iberian guillemots. Moreover, negative NAO values

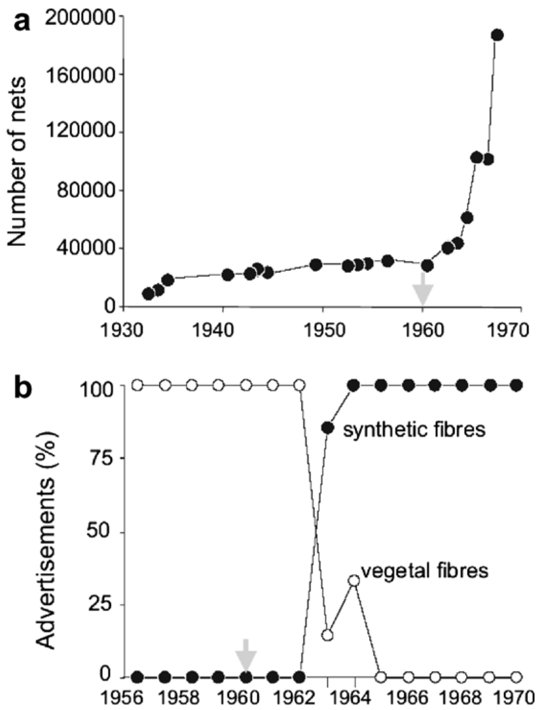

Fig. 7 – (a) Change in the number of entangling nets (gillnets and driftnets) in the coasts of Galicia, 1935–1968. (b) Percentage of advertisings offering synthetic or vegetal fishing gear in the monthly journal "Industrias Pesqueras". The arrow marks the beginning of the crash period for Iberian common guillemots (*Uria aalge*).

have been related to higher abundances of pelagic fish species in the Iberian Peninsula (Guisande et al., 2004). Indeed, the large pelagic fish landings during the population crash further suggest high abundance of pelagic fish species in this period.

Adult survival in guillemots is buffered against food shortages through behavioural changes (Monaghan et al., 1994; Bryant et al., 1999; Oedekoven et al., 2001 but see Oro and Furness, 2002). Although reduced food availability tends to have a much more dramatic effect on breeding success (Wanless et al., 2005), starvation due to prolonged periods of reduced food availability can also decrease adult survival (Bailey and Davenport, 1972; Piatt and Van Pelt, 1997). Nevertheless, fishery landings data does not support evidence of dramatic reductions in the availability of pelagic prey fish for Iberian guillemots in the crash period that could severely reduce adult survival. In contrast, the captures of the main pelagic fisheries, with the exception of anchovy, were abundant during the crash period. Even before the collapse of the anchovy fishery and despite higher market prices, anchovy landings were an order of magnitude inferior to that of sardine or mackerel, showed high interannual variability and concentrated in a few months, thus suggesting a relatively scarce and seasonal resource. Hence, it is unlikely that a sharp reduction in the availability of anchovies could have an important effect on the survival of adults.

The invention of synthetic fibres in the 1950s and other technological developments (e.g. hydraulic hauling equipment, electronic instrumentation) gave rise to significantly increased production of fisheries worldwide and substantially increased the fishing power of an individual fishing vessel (Caddy and Cochrane, 2001, Valdemarsen, 2001). Indirect effects upon the guillemot population due to a sudden increase in fishing effort in Atlantic Iberia are unlikely because pelagic prey fish landings remained within previous levels in the decades following the guillemot crash.

4.2. *Changes in human-related factors*

Ringing data suggests that human factors (shooting, drowning in nets and oil pollution) accounted for at least half

Table 3 – Ship wrecks involving the release into the sea of oil or other hazardous products in the Atlantic waters of the Iberian Peninsula since 1950

Vessel	Date	Spill type	Tonnes spilled	Location
Janina	18/01/57	Fuel	10,000	Vigo? (G)
Bonifaz	03/06/64	Oil undetermined	500	15 km off Fisterra (G)
Spyros Lemnos	08/11/68	Heavy crude	15,000	Fisterra (G)
Erkowitt	11/10/70	Dieldrin	286	Cabo Vilán (G)
Polycommander	04/05/70	Light crude	15,000	Illas Cíes (G)
Saint Mary	14/01/74	Fuel	3,000	400 km off Lisbon (P)
Jakob Maersk	29/01/75	Crude	84,000	Leixoes (P)
Urquiola	12/05/76	Crude	101,000	Coruña (G)
Andros Patria	01/01/78	Heavy crude	60,000	Sisargas (G)
Turgut Reis	25/12/79	Oil undetermined	224	170 km off Coruña (G)
Campeón	15/08/80	Fuel	Undetermined	Sines (P)
Ibsa Uno	27/04/80	Fuel	143	Marín (G)
Good Lord	19/12/83	Fuel	37	Langosteira (G)
Cason	05/12/87	Chemicals	1100	Fisterra (G)
Marao	14/07/89	Crude	600	Sines (P)
Aegean Sea	03/12/92	Light crude	66,800	Coruña (G)
Cercal	02/10/94	Light crude	1360	Port (P)
Enalios Thetis	01/10/98	Heavy crude	150	Sines (P)
Coral Bulker	25/12/00	Fuel and gasoil	700	Viana do Castelo (P)
Prestige	12/11/02	Fuel	77,000	5 km off Muxía (G)

G, Galicia, P, Portugal. Date is expressed as day/month/year.

(47%) of the mortality of wintering common guillemots in Atlantic Iberia. Furthermore, ringing data suggests that net-mortality was the most serious mortality factor. In the period when the Iberian guillemot population collapsed, vegetal nets were substituted by synthetic nets and, concurrently, the number of enmeshing nets increased exponentially as there was almost a fivefold increase in the number of fishing nets from 1962 to 1967. Common guillemots seemed to be particularly vulnerable to net mortality in many areas of their breeding range during the second half of the XX century (Tasker et al., 2000). In Newfoundland, for example, ringing schemes indicated that 13–20% of the breeding population was killed annually in gill nets in the early 1970s (Piatt et al., 1984). Synthetic fibres are much difficult to avoid by diving guillemots because they are harder to detect visually (Brandt, 1974) and, for example, visual barriers (highly visible mesh made of multifilament nylon seine twine) attached to the otherwise virtually invisible monofilament nylon drift gillnets, can effectively reduce the common guillemot bycatch (Melvin et al., 1999).

Oil pollution probably was another factor with a significant effect upon adult guillemot survival. Guillemots are especially prone to oiling because they spend most of their time swimming on the sea surface. It is not surprising thus, that in many instances, guillemots comprise the majority of casualties due to chronic and acute oil pollution (e.g. Piatt et al., 1990; Wiese and Ryan, 2003). It has been shown very recently that major oil spills doubled over-winter mortality of British adult guillemots wintering in Iberia (Votier et al., 2005). In the second half of the XX century the coasts of Iberia have suffered some of the worst oil disasters in the north Atlantic; however, most of the oil was spilled after the guillemot crash period. Nonetheless, one of the two major incidents involving oil spills in the crash period, the *Polycommander*, had the potential to severely affect the breeding population at Illas Cíes because it hit the colony in May. Oil spills close to breeding colonies have been shown to have a significant effect on breeding numbers (Ford et al., 1982; Hatchwell, 1988). However, it is unlikely that the *Polycommander* had a significant effect on the rest of the main guillemot colonies (e.g. Ortegal, Berlengas) because guillemots keep very close to the colonies in the breeding season (Cairns et al., 1987). The fact that the *Prestige* oil spill, in November 2002, killed large numbers of wintering Common Guillemots in Galicia and the Cantabrian (Votier et al., 2005) and that no breeding attempts were registered in the following years, may lead to the conclusion that this catastrophic event finished off the breeding population of the Common Guillemot in Galicia. It should be noted, however, that the 2002 season was also the last known breeding attempt for the population in Berlengas (ICN, 2006), hundreds of kilometers away from the area affected by the oil.

Another source of human-induced mortality for guillemots was shooting (Luis, 1982; Programa Arao, 1991). We have no data whatsoever to assess the relevance of hunting to Iberian common guillemots during the crash period. Hunting has significant effects upon population growth in parts of the breeding range of the species where traditional large-scale exploitation is practiced (e.g. Newfoundland and Labrador, Wiese et al., 2004; Greenland, Boertmann et al., 2004). In Spain the hunting season is open October to January and the number of hunting licenses almost doubled between 1975 and 1984 (no previous data; Munilla et al., 1991) suggesting a marked increase of hunting pressure in that period for wintering populations that probably ceased after the enforcement of hunting regulations after 1980.

4.3. *Final remarks*

The population modelling indicated that only an exceedingly high adult mortality rate can successfully reproduce the collapse observed between 1960 and 1974. The analysis of environmental and fishery data suggested better climate conditions and higher or sustained availability of pelagic prey fish in that period. In contrast, important human-related causes were affecting adult survival, including the rapid development of inshore gillnet fisheries that switched from vegetal to synthetic nets, probably the most serious threat to guillemots in Iberia and some other areas (Österblom et al., 2002; Olsson et al., 2000). Moreover, other known sources of mortality for adult guillemots, particularly oil pollution and shooting, probably added, in some extent, to the decline of the population between 1960 and 1974. Other unknown and undocumented factors, whether anthropogenic or environmental, could also have contributed to the decline of Iberian guillemots. Nevertheless, our analysis strongly suggests that human factors were affecting the population. Therefore, it is likely that conservation measures (e.g. fishing gear regulations in the vicinity of breeding colonies) could have rescued the Iberian population from the brink of extinction. The diagnosis leading to the assumption that climate change was responsible for the decline of the population did very little to reverse the situation and probably was counterproductive. Despite the alarming decline, no specific conservation measures (e.g. conservation plans) were provided and no actions were undertaken to mitigate the impact of anthropogenic threats.

Restoration plans, including the use of life-like decoys, recorded vocalizations, and other techniques to attract birds to a particular site where they may breed after a period of attendance have been proven to be effective for attraction and recolonization of common guillemots (Carter et al., 2003) and have been proposed for the restoration of Iberian guillemots (Velando and Freire, 1999b). However, as simulation models showed, the success of any reintroduction measures depends on good adult survival. A recent study on European Shags (*Phalacrocorax aristotelis*) strongly suggests that drowning in fishing nets continues to be a major threat for diving seabirds in Atlantic Iberia (Velando and Freire, 2002).

Low-latitude rear edge populations may be disproportionately important for the long-term conservation of genetic diversity, phylogenetic history and evolutionary potential of species (Petit et al., 2003; Hewitt, 2004). There is a risk of no conservation measures for low-latitude populations if it is assumed that they are doomed to extinction as a result of climate change because they are small or/and biogeographical outliers. This study highlights that to carelessly attribute (i.e. without an appropriate analysis) the decline of rear edge populations to climate change could be highly misleading if the population is suffering from other, particularly human, threats.

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