

Ecological impact of the “*Erika*” oil spill: Determination of the geographic origin of the affected common guillemots

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Abstract – Between 80 000 and 150 000 marine birds wintering in the Bay of Biscay were killed during the “*Erika*” oil spill. Three complementary studies were conducted to investigate the geographic origins of these birds. The common guillemot, *Uria aalge*, represented more than 80% of the oiled birds and these studies thus focused primarily on this species. Analyses of 184 ring recoveries and biometry of 1851 corpses indicated that guillemots originated from a large geographic area, including colonies from across the British Isles and the North Sea, along with more northern localities. However, the majority of individuals came from colonies located between western Scotland and the Celtic Sea. The third study, based on a population genetic approach using microsatellite markers (samples from dead oiled birds and from more than 600 birds caught in 19 breeding colonies), showed little genetic differentiation among north-eastern Atlantic guillemot colonies. This result limits the ability to identify the geographic origins of the birds using only DNA samples, but reveals a significant amount of gene flow among colonies. Overall, results indicate the large spatial scale of the oil spill's impact and underline the usefulness of combining multiple approaches to assess the local and regional effects of such accidents.

Key words: Oil spill / Ring recoveries / Biometrics / Genetics / Seabird / *Uria aalge* / Atlantic Ocean

Résumé – Détermination de l'origine géographique des guillemots de Troïl victimes de la marée noire du pétrolier « *Erika* ». La marée noire de l'« *Erika* » a décimé plus de 80 000 oiseaux marins hivernant dans le golfe de Gascogne, avec une estimation maximale de 150 000 victimes. Trois études complémentaires ont été mises en place pour évaluer l'origine géographique des oiseaux impactés. Le guillemot de Troïl, *Uria aalge*, représente à lui seul plus de 80 % des oiseaux mazoutés et ces travaux concernent principalement cette espèce. Il s'agit de l'analyse des reprises d'oiseaux bagués (portant sur 184 guillemots bagués comme poussins et retrouvés échoués), d'une étude biométrique (réalisée sur 1851 cadavres) et d'une étude génétique (réalisée sur des échantillons d'oiseaux échoués et sur plus de 600 prélèvements provenant de 19 colonies de reproduction). Les résultats des deux premières études montrent que les guillemots sont originaires d'une vaste zone géographique, englobant l'ensemble des colonies des îles Britanniques et de mer du Nord ainsi que des colonies plus septentrionales, mais en proportion variable. En effet, la grande majorité des oiseaux touchés est principalement originaire des colonies situées entre l'ouest de l'Écosse et la mer Celtique. La troisième approche a utilisé des marqueurs génétiques neutres (microsatellites). Elle montre une faible structuration génétique des populations, ce qui limite les possibilités d'identifier par cette méthode l'origine géographique des guillemots, mais souligne l'importance des flux de gènes entre colonies à l'échelle de l'Europe du nord. L'ensemble de ces résultats montre la grande étendue géographique de l'impact de la marée noire et souligne l'intérêt de combiner des approches à différentes échelles pour préciser les effets locaux et régionaux d'un tel accident pétrolier.

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1 Introduction

On the 12th of December 1999, the tanker *Erika* broke up in the north of the Bay of Biscay, off the coast of Brittany. The amount of oil released at sea was about 20 000 tonnes and more than 400 km of the French coast was impacted with various degrees of oil pollution. The first oiled birds were found in the northern part of the Bay of Biscay between the 14th and the 18th of December (Cadiou et al. 2003a). From the available data compiled for the national assessment of the seabird wreck and mortality following the oil spill ("*Bilan national des échouages et de la mortalité des oiseaux*"; Cadiou et al. 2003a), about 74 000 oiled birds (32 000 alive and 42 000 dead, mainly seabirds and seaducks) were recorded ashore along the coast of the Bay of Biscay. As in the case of other oil spills (Piatt and Lenski 1989; Heubeck et al. 2003), determining the geographic origin of these birds is of major importance if one wants to assess the ecological impact of the oil spill. One species, the common guillemot *Uria aalge* represented 83% of the birds killed. The French breeding population of the common guillemot is limited to only a few hundred pairs breeding in Brittany (Cadiou 2002), but several million pairs of this species breed along the coasts of northern Europe (Harris and Wanless 2004), which underlines the need to identify the origin of the birds.

Amongst other studies financed by the French government within the scientific network set up to assess the consequences of the *Erika* oil spill, three concerned the determination of the geographic origin of the seabirds killed after the wreck. They were based respectively on analyses of ring recoveries, biometrics of birds and genetic data. This paper presents the results obtained for the common guillemot.

2 Materials and methods

2.1 Ring recoveries

Ringed birds were collected and recorded by various people or rehabilitation centres receiving oiled birds. However, due to the difficulty to detect ring on heavily oiled birds or to the lack of organization, it appeared that about half of the ringed birds have not been recorded (Cadiou and Dehorter 2003). Data were centralized by "Bretagne Vivante" and CRBPO ("*Centre de recherches sur la biologie des populations d'oiseaux*", Museum National d'Histoire Naturelle, Paris) and sent to ringing centres abroad to obtain information on the date and locality of ringing, and the age of the birds at ringing.

2.2 Biometrics

About 2300 corpses of oiled birds collected directly on the coast or coming from rehabilitation centres were used for the biometric study. The study sample included 1851 common guillemots. During external and internal examinations, several measurements were made according to standardized methods (Hope Jones et al. 1982a; Camphuysen 1995). Many species of bird exhibit phenotypic variation in structural size or plumage

pattern that can be related to their natal area and thus can be used to identify the origin of birds killed during an oil spill (Hope Jones et al. 1982b; Anker-Nilssen et al. 1988; Weir et al. 1997). Some body characters can also vary according to age or sex, allowing to infer information on the structure of the affected group of birds (sex-ratio, age ratio, sexual maturity). In the common guillemot, there is a latitudinal gradient in upper parts colour and wing length, birds originating from northern colonies being darker and having longer wings (Cramp 1985; Hope Jones 1988). Data on plumage colour and wing length of mature birds from the oil spill were thus compared to what is known about these latitudinal variations. Comparisons were made according to the sex of individuals as males and females differ in size. The cloacal bursa (or bursa of Fabricius) is an organ well developed in young birds (Møller and Erritzøe 2001). Seemingly, white tips on underwing coverts are present in first-year guillemots (Camphuysen 1995; Cadiou et al. 2003b). Thus these two variables were considered as surrogates of the age of a bird. The sample included 952 females, 695 males and 204 unsexed birds and all measurements were not always available for all the birds.

2.3 Genetic data

DNA can be extracted from the tissue of birds recovered dead or alive following an oil spill and the corresponding genetic information could be used to determine the origin of the birds. The objective of the third approach was thus to test whether it was possible to assign individuals to their breeding area of origin using an assignment method (Cornuet et al. 1999) and data on the genotypes of individuals from the oil spill and from breeding colonies (Riffaut et al., unpublished). Such an approach is dependent on the ability to genetically characterize sub-groups of individuals. The application of such an approach was attempted because of the potentially genetically structured populations of seabirds (associated with their high philopatry and the description of phenotypically distinct groups) and the recent availability of highly polymorphic markers (microsatellites), which appeared to be promising to use in this context (Edwards et al. 2001). The method uses the allele frequencies of each sampled population to compute the probability of occurrence of the multi-locus genotype of individuals within each population.

In order to genotype individuals, DNA was extracted from blood, growing feathers or muscle tissue (in the case of dead birds). The study involved two main steps (Riffaut et al., unpublished). First, the genetic structure of the north-Atlantic populations of common guillemots was investigated using 6 microsatellites markers (Ibarguchi et al. 2000; Tirard et al. 2002) and more than 600 birds sampled from 19 colonies from the north-east of the Atlantic Ocean (Fig. 1). Second, to assess the reliability of the assignments tests for determining the geographic origin of the oiled birds, we then attempted to assign the individuals sampled in the 19 different candidate colonies to their population of origin. We also used the same method to attempt to assign 48 ringed guillemots recovered following the oil spill. The test of the approach on birds of known origin was needed before considering any attempt on the large number of samples collected from oiled birds.

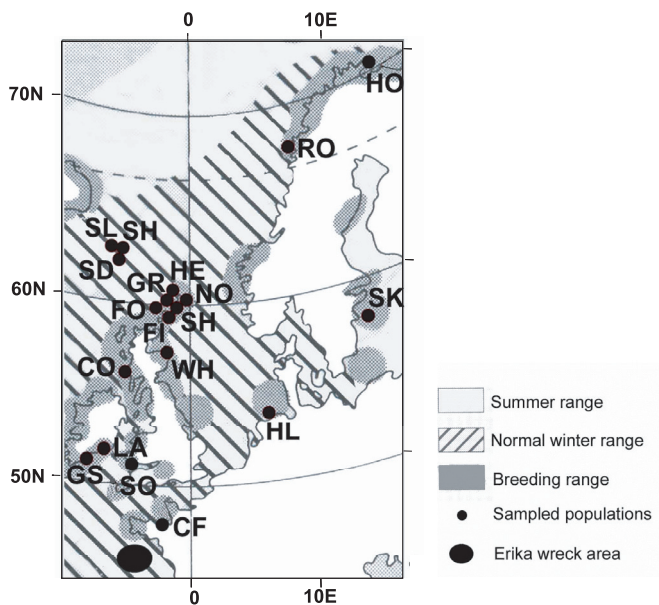


Fig. 1. Distribution of common guillemot, *Uria aalge*, populations in the north-east Atlantic and sampling locations (black circles) for the population genetic study.

3 Results

3.1 Ring recoveries

Amongst the 266 ringed birds recorded during the oil spill, there were about three third of common guillemots, out of which 184 had been ringed as chicks before fledging from their colony of birth. The age and the geographic origin of these latter birds are thus known with certainty. Their age ranged from less than 1 to 18 years old (i.e. born from 1981 to 1999) but 34% and 29% were young birds ringed in 1999 and 1998 respectively. Amongst these individuals, 90 originated from colonies located in western Scotland, 64 from south-eastern Irish colonies, 17 from Welsh colonies, 7 from northern Scotland colonies and the remaining 6 from colonies bordering the North Sea (4 from Britain and 2 from Helgoland, Germany; Fig. 2).

However these results are raw data which need to be considered in relation to the location of the different colonies where ringing activities occurred in the north-east Atlantic and the number of chicks ringed annually on these colonies. Indeed, ringing does not occur on all colonies and ringing effort is not proportional to the abundance of the local breeding populations (Harris and Swann 2002). Thus, these figures do not reflect the real proportion of the birds originating from the different geographic areas.

3.2 Biometrics

It was tested whether the wing length varied statistically according to the sex, the upperparts colour (brown or dark), the presence of the cloacal bursa and the tip pattern of underwing coverts (presence or absence of white tips). Results of the multivariate analysis showed an effect of the four variables but not

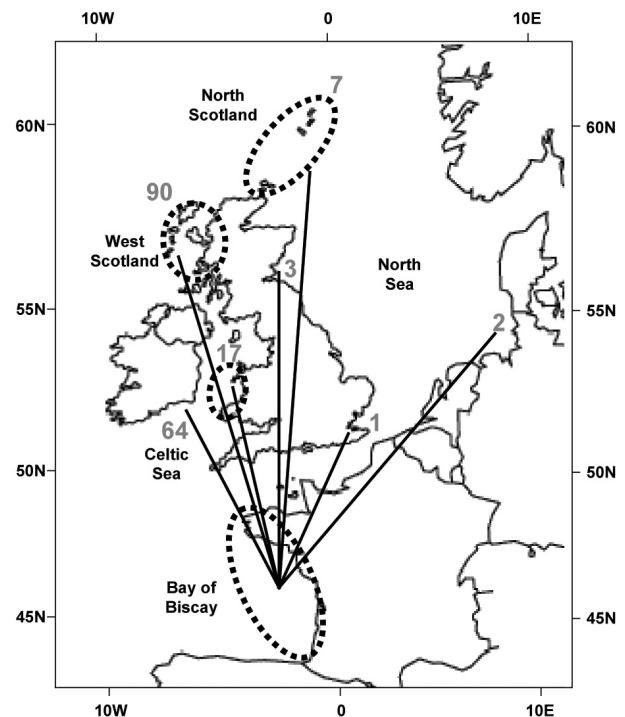


Fig. 2. Geographic origin of the 184 common guillemots, *Uria aalge*, ringed as chicks and recovered in the Bay of Biscay during the *Erika* oil spill (from Cadiou and Dehorter 2003).

of their interactions (SAS GLM procedure; sex: $F_{1,159} = 7.00$, $p < 0.01$; upperparts colour: $F_{1,159} = 4.39$, $p < 0.05$; cloacal bursa: $F_{1,159} = 15.56$, $p < 0.0001$; underwing coverts: $F_{1,159} = 7.86$, $p < 0.01$; $N = 164$ birds). Females had longer wings than males; older birds had longer wings than young birds and darkish birds have longer wings than brownish birds (Table 1). Differences also existed for head length, bill length and bill depth, older darkish males tending to be the larger individuals (Table 1).

Mean wing lengths were then compared with data obtained on breeding guillemots originating from different colonies of the north-east Atlantic. Only sexually mature birds (without cloacal bursa) of the *Erika* sample were taken into account because immature birds are smaller, especially first year birds (Table 1). Both sexes were considered separately (Fig. 3). A distinction was also made between birds with blackish or brownish upperparts. Results showed that *Erika*'s brownish birds had wing lengths situated between those of breeding birds from the Celtic Sea and from western Scotland (Fig. 3). The blackish birds probably originated from Scotland as well as potentially from colonies located in the Faeroe Islands and south-western Norway. Amongst these birds, there are also a few females with long wings which could come from much more northern colonies.

3.3 Genetic data

Overall, the level of population genetic differentiation, estimated using F-statistics, was very weak (average $F_{st} = 0.004$, $p = 0.0108$, 95% C.I. = 0.001–0.008). A plot of isolation by

Table 1. Biometrics of common guillemots collected during the *Erika* oil spill according to sex, upperparts colour, cloacal bursa and tip pattern of underwing coverts. Mean $\pm$ standard deviation (mm), sample size in brackets, range in square brackets.

Sex	Upper- parts colour	Cloacal bursa	White tip of underwing coverts	Wing length	Head length	Bill length	Bill depth
Female	Brown	Presence	Presence	197.1 $\pm$ 5.5 (11)	108.9 $\pm$ 3.4 (32)	46.2 $\pm$ 2.8 (32)	11.6 $\pm$ 0.7 (32)
				[188-205]	[100.0-114.9]	[40.0-52.1]	[10.3-13.6]
			Absence	200.1 $\pm$ 5.8 (19)	110.5 $\pm$ 2.8 (38)	46.9 $\pm$ 2.2 (38)	11.9 $\pm$ 0.5 (38)
				[192-212]	[105.0-115.5]	[41.5-50.1]	[11.1-13.0]
		Absence	Presence	202.0 $\pm$ 7.9 (3)	110.9 $\pm$ 3.1 (9)	45.8 $\pm$ 2.9 (9)	12.4 $\pm$ 0.7 (9)
				[193-208]	[107.0-115.0]	[41.0-50.4]	[11.3-13.4]
			Absence	204.0 $\pm$ 4.9 (19)	110.2 $\pm$ 2.5 (34)	46.8 $\pm$ 2.6 (34)	12.1 $\pm$ 0.6 (34)
				[197-213]	[105.0-116.0]	[40.4-51.3]	[10.9-13.6]
	Dark	Presence	Presence	202.6 $\pm$ 4.2 (5)	109.1 $\pm$ 3.9 (6)	45.0 $\pm$ 2.6 (6)	11.6 $\pm$ 0.9 (6)
				[198-208]	[105.0-115.5]	[41.6-49.1]	[11.0-13.3]
			Absence	202.9 $\pm$ 4.8 (13)	111.8 $\pm$ 2.3 (24)	47.8 $\pm$ 2.1 (24)	12.1 $\pm$ 0.6 (24)
				[196-211]	[107.0-116.0]	[41.8-51.2]	[10.6-13.5]
		Absence	Presence	207.0 (1)	113.0 $\pm$ 0.0 (2)	47.6 $\pm$ 1.3 (2)	12.5 $\pm$ 0.8 (2)
					[113.0]	[46.7-48.5]	[11.9-13.1]
			Absence	206.1 $\pm$ 6.5 (22)	111.9 $\pm$ 2.9 (32)	47.4 $\pm$ 2.5 (32)	12.6 $\pm$ 0.5 (32)
				[195-220]	[107.0-118.5]	[42.6-54.3]	[11.9-13.7]
	Total female	–	–	202.6 $\pm$ 6.2 (93)	110.6 $\pm$ 3.0 (177)	46.8 $\pm$ 2.5 (177)	12.1 $\pm$ 0.7 (177)
Male	Brown	Presence	Presence	195.7 $\pm$ 4.4 (17)	111.8 $\pm$ 2.7 (41)	47.4 $\pm$ 2.4 (41)	11.9 $\pm$ 0.6 (41)
				[188-220]	[100.0-118.5]	[40.0-54.3]	[10.3-13.7]
			Absence	198.8 $\pm$ 4.9 (23)	113.8 $\pm$ 3.6 (40)	47.4 $\pm$ 2.4 (41)	11.9 $\pm$ 0.6 (41)
				[188-203]	[104.0-116.0]	[40.8-51.5]	[10.8-13.5]
		Absence	Presence	201.0 (1)	114.5 $\pm$ 4.5 (6)	48.8 $\pm$ 3.6 (6)	12.2 $\pm$ 0.6 (6)
				[192-214]	[107.0-121.0]	[43.0-53.0]	[11.1-13.6]
			Absence	202.2 $\pm$ 6.8 (13)	113.4 $\pm$ 3.7 (21)	49.3 $\pm$ 2.6 (40)	12.4 $\pm$ 0.5 (40)
				[192-214]	[107.5-121.0]	[45.0-53.5]	[11.3-14.4]
	Dark	Presence	Presence	190.0 (1)	112.0 $\pm$ 0.9 (3)	50.2 $\pm$ 0.3 (3)	11.4 $\pm$ 0.5 (3)
				[195-203]	[111.0-112.5]	[49.9-50.5]	[11.0-11.9]
			Absence	198.8 $\pm$ 3.1 (6)	113.3 $\pm$ 2.3 (10)	48.7 $\pm$ 2.2 (10)	12.2 $\pm$ 0.6 (10)
				[195-203]	[110.0-117.5]	[45.5-52.6]	[11.2-13.1]
		Absence	Presence	195.5 $\pm$ 6.4 (2)	112.5 $\pm$ 2.3 (3)	47.6 $\pm$ 1.9 (3)	12.5 $\pm$ 0.7 (3)
				[191-200]	[110.0-114.5]	[45.8-49.5]	[11.7-12.9]
			Absence	204.6 $\pm$ 5.8 (8)	114.6 $\pm$ 3.1 (20)	49.7 $\pm$ 2.8 (20)	12.8 $\pm$ 0.6 (20)
				[197-214]	[110.0-119.0]	[44.9-54.5]	[11.5-13.8]
	Total male	–	–	199.2 $\pm$ 5.9 (71)	113.2 $\pm$ 3.3 (144)	48.6 $\pm$ 2.6 (144)	12.4 $\pm$ 0.8 (144)
				[188-214]	[104.0-121.0]	[40.8-54.5]	[10.8-14.4]

Birds with cloacal bursa and white tip of underwing coverts are mainly first winter birds; birds without cloacal bursa and white tip of underwing coverts are sexually mature birds and others are mainly immature birds (2–4 years old).

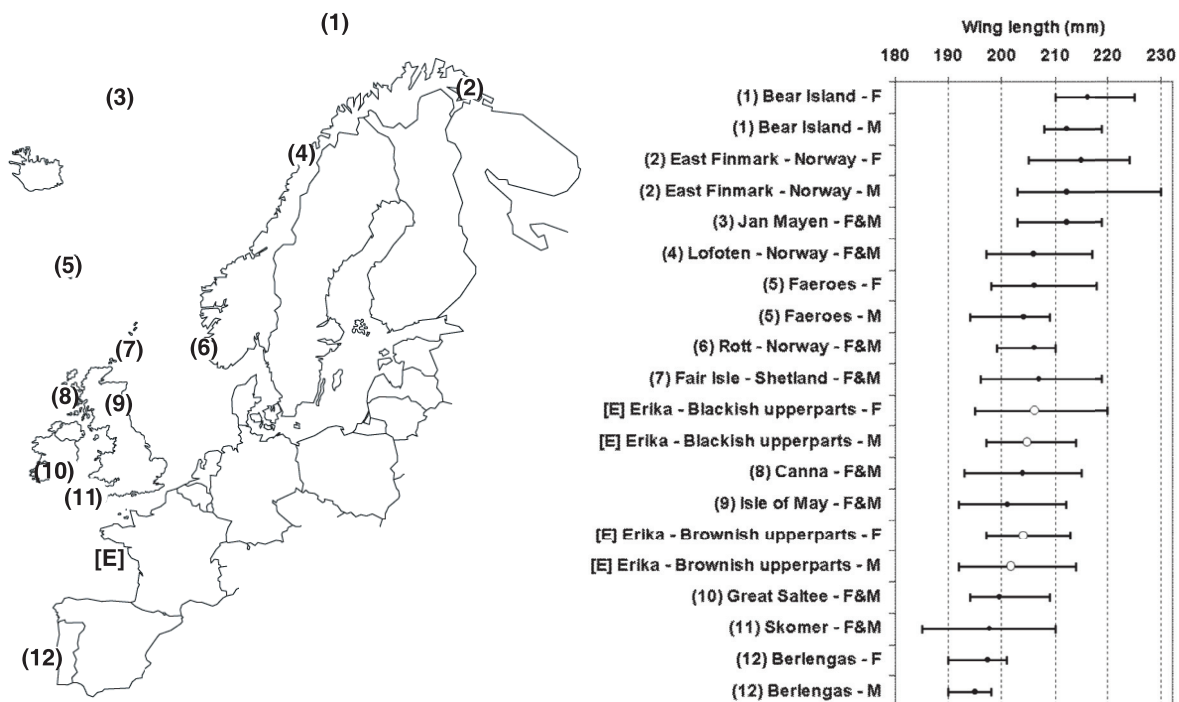


Fig. 3. Mean wing lengths (with range) of adults common guillemots, *Uria aalge*, originating from different colonies in the north-east Atlantic and of adults killed during the *Erika* oil spill (F = female; M = males; from Pethon 1967; Cramp 1985; Hope Jones 1984, 1988b; Camphuysen 1989; Cadiou et al. 2003b; R. Barrett pers. comm.).

distance revealed a weak positive correlation between genetic and geographic distances ($p = 0.047$). This pattern of isolation by distance was much stronger when the samples from a colony of the western Atlantic (Witless Bay, Newfoundland, Canada) were included in the analyses (Riffaut et al., unpublished). Nevertheless, the low level of population genetic structure prevented to determine reliably the origin of the oiled birds: the results of the assignment tests showed that individuals from the breeding colonies could not be assigned reliably to the colony in which they had been sampled (less than 6% of the individuals were assigned to the population in which they had been sampled). Further, the ringed birds recovered following the oil spill could not be assigned reliably to the colonies of the region in which they had been ringed: a great majority of the 48 ringed birds could be assigned to several areas of origin despite the fact that 47 had been ringed in the British isles and one on the island of Helgoland, Germany (Fig. 4). These results were relatively disappointing given the wide area of origin of the recovered birds, the polymorphism of the microsatellite markers and the large spatial scale of the sampling of colonies (from Brittany in the south, to northern Norway in the north-east).

4 Discussion

The common guillemots killed during the *Erika* oil spill originated from a large geographic area of the north-east Atlantic. However, the great majority came from colonies located between western Scotland and the Celtic Sea. A lower

proportion originated from colonies alongside the North Sea, but also very likely from the Faeroe Islands or south-western Norway. A much smaller proportion could have originated from more northern colonies.

It was already known from ring recoveries that most of the young guillemots from Scotland spent their first winter in the North Sea while those from the Celtic Sea winter in the Bay of Biscay (Swann and Ramsey 1983; Harris and Swann 2002). Analyses of ring recoveries during the *Erika* oil spill confirmed this pattern of distribution (Cadiou and Dehorter 2003). However, more data are still needed to estimate the proportion of birds from different origins which winter in the northern Bay of Biscay. Indeed, the pattern of dispersal of common guillemots after the breeding season is complex and varies according to their geographic origin, their age and probably their sex (Brown 1985; Harris and Swann 2002). Also, prior to the *Erika* oil spill, there was no estimate of the number of common guillemots at sea in the Bay of Biscay in winter. The first large scale aerial surveys started in the winter 2000–2001 (Bretagnolle et al. 2004). Therefore, it remains difficult to assess the potential impact of the mortality induced by the *Erika* oil spill on the demography of the common guillemot in British and Irish colonies. On a short term time scale, no major decrease in breeding numbers has been recorded in different study colonies around the British Isles (Mavor et al. 2003).

The oil spill toll appears very high for common guillemots, with casualties ranging from 50 000 to 125 000 for recorded and estimated numbers respectively, including extrapolations for stranded corpses not counted on the coast and corpses lost at sea (see details in Cadiou et al. 2003a). However the

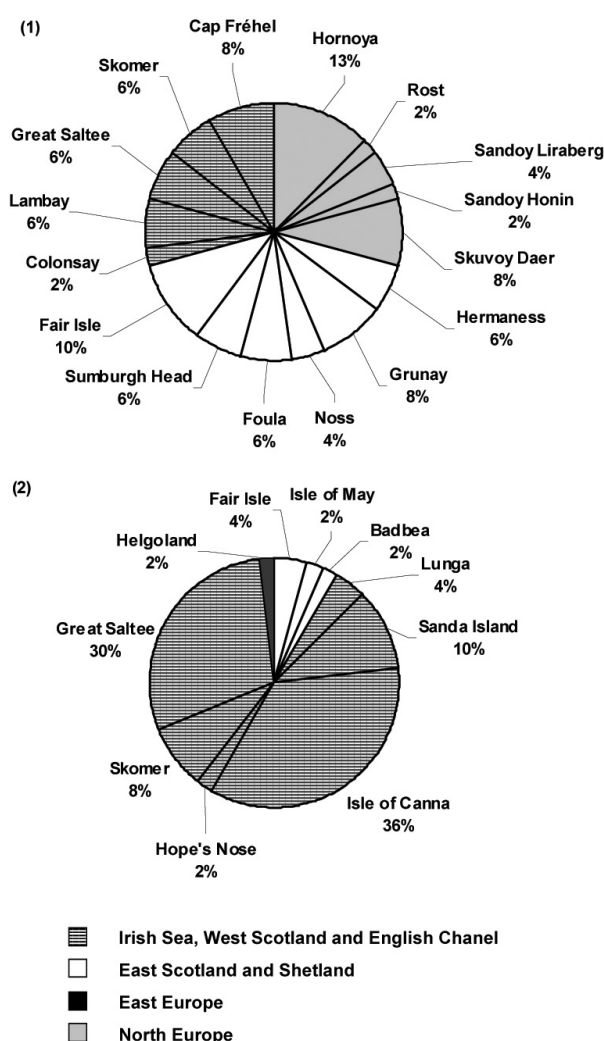


Fig. 4. Origin of the 48 oiled ringed common guillemots, *Uria aalge*, according to (1) the direct assignment method and (2) the “true” origin of these oiled birds obtained from ring recovery data. For the direct assignment method, the 19 candidate populations were grouped by geographic region: Irish Sea, West Scotland and English Channel (Lambay, Great Saltee, Skomer and Cap Fréhel); East Scotland and Shetland (Hermaness, Grunay, Noss, Foula, Sumburgh Head, Fair Isle and Whinniford); East Europe (Stora Karlsø and Helgoland) and North Europe (Hornøya, Røst, Sandoy Liraberg, Sandoy Honin and Skuvoy Daer). These same geographic groupings are indicated for the true origins of the ringed birds.

demographic impact on the population could be far less obvious especially because two main factors, the geographic area of origin and the age structure of the birds, contribute to mitigate the effect. Firstly, the potential area of origin held more than one million breeding pairs in 1999, with 250 000 of them in the main area of origin, i.e. from the west of Scotland to the Celtic Sea (Harris and Wanless 2004). The mean annual rate of increase of guillemot populations in Britain and Ireland is 2% (Harris and Wanless 2004), the mean productivity is 0.7 chick per breeding pair (Mavor et al. 2003), the survival rates is 46% during the first year of life, 75% during the second year, 88% during the third year and 95% afterwards

(Wernham et al. 1997; Harris et al. 2000) and breeding generally does not occur until birds are 5–6 years old (Harris et al. 1994). Taking into account these parameters, it can be estimated that the total number of birds from the main area of origin was about 900 000 (500 000 breeders + 400 000 pre-breeders respectively, i.e. 175 000 juveniles born in 1999 and 225 000 immatures born between 1995 and 1998), out of which only an unknown proportion was effectively wintering in the north of the Bay of Biscay at the time of the *Erika* oil spill. Secondly, most of the common guillemots killed were non-breeders that might have been recruited a few years later, with about one third of first winter birds, one third of older sexually immature birds and one third of sexually mature birds (Cadiou et al. 2003b; see also Table 1). Moreover, the precise breeding status of these latter birds remains unknown and they could be potential first-time breeders or experienced breeding adults.

Although the use of the population genetic approach did not help efficiently to determine the geographic origin of the oiled birds, this study provided some important information about the genetic structure and functioning of common guillemot populations in the North Atlantic. From a genetic viewpoint, such results suggest that a management unit could in fact be the whole North Atlantic population (Friesen et al. 1997; Hedrick 2001). The weak genetic differentiation at this spatial scale revealed using highly polymorphic microsatellite markers indeed shows that the colonies constitute a largely panmictic population. This idea supports previous results obtained using mitochondrial markers (Moum et al. 1991; Friesen et al. 1996; Friesen 1997; Moum and Arnason 2001). Moreover, the results suggest that, despite the fact that a large number of common guillemots were killed due to the *Erika* oil spill, little genetic variation is likely to have been lost. Despite a supposedly extreme rate of philopatry for this species (Tuck 1960; Hudson 1985; Harris and Wanless 1995; Harris et al. 1996a,b), the lack of strong population structure observed can be due to a historically recent expansion of the populations or can be the direct result of intercolony dispersal. Dispersal can oppose the effect of the genetic drift and tends to genetically homogenize populations (Slatkin 1989). Intercolony dispersal has been assumed for some common guillemot populations in which colony size increased too quickly to be explained solely by the intrinsic growth rate (Tuck 1960; Evans and Nettleship 1985; Harris and Wanless 2004). Resightings of ringed birds have also suggested that auks, including the common guillemot, can move and disperse between breeding colonies at large spatial scales (Halley and Harris 1993; Lyngs 1993; Kampp and Falk 1998; R. Barrett, pers. comm.). If emigrants breed successfully with local individuals, they may lead to sufficient gene flow to homogenize gene frequencies (Wright 1931; Hedrick 1999). Significant intercolony dispersal could mean that common guillemot populations have a strong capacity to recover after local disasters. The interplay between behavioural and demographic processes is nevertheless important to consider (Boulinier and Lemel 1996). It has for instance been suggested that some type of population resilience may indeed be a consequence of dispersal (Cairns and Elliot 1987; Wiens 1996; Wiens et al. 1996) combined with increased access to breeding for first-time breeders due to the availability of vacant sites

(Croxall and Rothery 1991). In species in which individuals show an attraction to conspecifics, a critical situation may nevertheless happen when local breeding groups decrease below a certain threshold size. Recruiting to an empty site is different than recruiting in an existing colony and an important question is the time it may take for a species to re-colonize an area following local extinction.

The comparison of the results obtained in the context of the *Erika* oil spill with those following the *Prestige* oil spill, which occurred three years later than the wreck of *Erika* in the south-western part of the Bay of Biscay, should be very interesting. Indeed, once again, the common guillemot was the most impacted species (Camphuysen et al. 2002; García et al. 2003).

Complementary analyses based on stable isotopes could also be used to determine the origin of birds (e.g. Hobson 1999; Chérel et al. 2000; Lott et al. 2003). Samples of feathers, especially from common guillemots and divers *Gavia* spp., have been collected and stored during the *Erika* oil spill in order to investigate the usefulness of this tool on a conservation viewpoint.

5 Conclusion

The results obtained underline that for a full assessment of the ecological impact of an oil spill on seabird populations, it is necessary to combine information on the dynamics of the distribution of seabirds at sea with knowledge of the different processes involved in the dynamics of the subdivided breeding populations. Investigations using model simulations under different scenarios should help integrating the available information for seabirds sensitive to oil pollution (Ford et al. 1982; Seip et al. 1991). In the case of oil spills, which occur often at a time when birds are dispersed away from the colonies, not only the age and sex structure of the population must be considered, but also the potential mixing of different subgroups which will vary with the time of the year. Such a modelling approach should allow one to use the available information to assess the potential consequences of a specific oil spill on different seabird populations, but also more generally to determine the scale and type of data needed to assess the potential impact on the breeding populations.

During an oil spill, three points relevant to birds should be carefully investigated in order to allow an ecological impact assessment on a short, medium or long term scale. First, all available data should be centralized and analysed to obtain the total number of living or dead oiled birds collected on the coast and, as far as possible, to estimate the global mortality. Second, studies should be conducted to determine the geographic origins of the birds. Third, studies should also be conducted to determine the population structure of the species impacted (sex-ratio, age ratio and sexual maturity). Indeed, as seabirds are long-lived species exhibiting deferred maturity, the demographic impact of massive mortality would not be the same if the majority of the victims are young non-breeding birds or breeding adults (Croxall and Rothery 1991; Russell 1999).

Mass mortality during oil spill offer opportunity to obtain large samples of seabirds for different studies and this biological material should not be wasted. Indeed, due to technical,

legal or ethical reasons it is impossible to take such samples under normal circumstances.

Experience from the *Erika* oil spill has highlighted problems and gaps and the crucial need of more coordination between administrative authorities, scientists and rehabilitation centres receiving oiled birds (Cadiou et al. 2003a,b). Pre-planning is essential to allow an immediate and relevant response and to avoid the lack of preparedness as during the *Erika* and *Prestige* oil spills (Cadiou et al. 2003a; Heubeck et al. 2003).

Complementary studies based on classical methods (ring recoveries and biometrics) or more recent techniques (genetic and stable isotopes) appear essential to improve the determination of the geographic origins of birds of different species. Seabird corpses stranded on the coast in winter should be considered as a valuable biological material in order to increase data collection (Camphuysen and van Franeker 1992). All these studies would allow giving more precise answers and would contribute to better oil spill impact assessment in the future.

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References

- Anker-Nilssen T., Hope Jones P., Røstad O.W., 1988, Age, sex and origins of auks (Alcidae) killed in the Skagerrak oiling incident of January 1981. *Seabird* 11, 28-46.
- Bretagnolle V., Certain G., Houte S., Métais M., 2004, Distribution maps and minimum abundance estimates for wintering auks in the Bay of Biscay, based on aerial surveys. *Aquat. Living Resour.* 17, 353.
- Boulinier T., Lemel J.-Y., 1996, Spatial and temporal variations of factors affecting breeding habitat quality in colonial birds: some consequences for dispersal and habitat selection. *Acta Oecol.* 17, 531-552.

- Brown R.G.B., 1985, The atlantic alcidae at sea. In: Nettleship D.N., Birdhead T.R. (Eds.), The Atlantic Alcidae. Academic Press, London, pp. 383-426.
- Cadiou B., 2002, Oiseaux marins nicheurs de Bretagne. Les cahiers naturalistes de Bretagne No 4. Conseil Régional de Bretagne, Éditions Biotope, Mèze.
- Cadiou B., Dehorter O., 2003, Marée noire de l'Erika – Contribution à l'étude de l'impact sur l'avifaune. Analyse des reprises/contrôles de bagues. Rapport Bretagne Vivante-SEPNB, CRBPO, DIREN Bretagne.
- Cadiou B., Chenesseau D., Joslain H., 2003a, Marée noire de l'Erika – Contribution à l'étude de l'impact sur l'avifaune. Bilan national des échouages et de la mortalité des oiseaux (BNEMO). Rapport Bretagne Vivante-SEPNB, LPO Loire-Atlantique, Observatoire des marées noires, DIREN Bretagne.
- Cadiou B., Cam E., Fortin M., Monnat J.-Y., Gélinaud G., Cabelguen J., Le Roch A., 2003b, Impact de la marée noire de l'Erika sur les oiseaux marins migrateurs : détermination de l'origine et de la structure des populations par la biométrie. Rapport Bretagne Vivante-SEPNB, DIREN Bretagne.
- Cairns D.K., Elliot R.D., 1987, Oil spill impact assessment for seabirds: the role of refugia and growth centers. Biol. Cons. 40, 1-9.
- Camphuysen C.J., 1989, Biometrics of auks at Jan Mayen. Seabird 12, 7-10.
- Camphuysen C.J., 1995, Leeftijdsbepaling van Zeekoet *Uria aalge* en Alk *Alca torda* in de hand. Sula 9, 1-22.
- Camphuysen C.J., van Franeker J.A., 1992, The value of beached bird surveys in monitoring marine oil pollution. Technisch rapport Vogelbescherming 10, Vogelbescherming Nederland, Zeist.
- Camphuysen C.J., Heubeck M., Cox S.L., Bao R., Humple D., Abraham C., Sandoval A., 2002, The *Prestige* oil spill in Spain. Atlantic Seabirds 4, 131-140.
- Chérel Y., Hobson K.A., Weimerskirch H., 2000, Using stable-isotope analysis of feathers to distinguish moulting and breeding origins of seabirds. Oecologia 122, 155-162.
- Cornuet J.M., Piry S., Luikart G., Estoup A., Solignac M., 1999, New methods employing multilocus genotypes to select or exclude populations as origins of individuals. Genetics 153, 1989-2000.
- Cramp S. (Ed.), 1985, The Birds of the Western Palearctic, Vol. IV. Oxford University Press, Oxford, London, New York.
- Croxall J.P., Rothery P., 1991, Population regulation of seabirds: implications of their demography for conservation. In: Perrins C.M., Lebreton J.-D., Hiron G.J.M. (Eds.), Bird population studies: relevance to conservation and management. Oxford University Press, Oxford, pp. 272-296.
- Edwards S.V., Siva M.C., Burg T., Friesen V., Warheit K.I., 2001, Molecular genetic markers in the analysis of seabird bycatch populations. In Proceedings – Seabird bycatch: Trends, roadblocks and solutions. University of Alaska Sea Grant, pp. 115-140.
- Ford R.G., Wiens J.A., Heineman D., Hunt G.L., 1982, Modelling the sensitivity of colonially breeding marine birds to oil spills: guillemot and kittiwake populations on the Pribilof Islands, Bering Sea. J. Appl. Ecol. 19, 1-31.
- Friesen V.L., Montevicchi W.A., Baker A.J., Barrett R.T., Davidson W.S., 1996, Population differentiation and evolution in the common guillemot *Uria aalge*. Mol. Ecol. 5, 793-805.
- Friesen V.L., 1997, Population genetics and the spatial scale of conservation of colonial waterbirds. Colon. Waterbird 20, 353-368.
- García L., Viada C., Moreno-Opo R., Carboneras C., Alcade A., González F., 2003, Impacto de la marea negra del *Prestige* sobre las aves marinas. SEO/Birdlife, Madrid.
- Halley D.J., Harris M.P., 1993, Intercolony movement and behaviour of immature Guillemots *Uria aalge*. Ibis 135, 264-270.
- Harris M.P., Halley D.J., Swann R.L., 1994, Age of first breeding in Common Murres. Auk 111, 207-209.
- Harris M.P., Halley D.J., Wanless S., 1996a, Philopatry in the Common Guillemot *Uria aalge*. Bird Study. 43, 134-137.
- Harris M.P., Wanless S., 1995, Survival and non-breeding of adult Common Guillemots *Uria aalge*. Ibis 137, 192-197.
- Harris M.P., Wanless S., Barton T.R., 1996b, Site use and fidelity in the Common Guillemot *Uria aalge*. Ibis 138, 399-404.
- Harris M.P., Swann B., 2002, Common guillemot. In: Wernham C.V., Toms M.P., Marchant J.H., Clark J.A., Siriwardena G.M., Baillie S.R. (Eds.), The migration atlas: movements of birds of Britain and Ireland. T. & A.D. Poyser, London, pp. 397-400.
- Harris M.P., Wanless S., 2004, Common guillemots *Uria aalge*. In: Mitchell, I., Newton, S., Ratcliffe, R., Dunn, T.E. (Eds.), Seabird populations of Britain and Ireland. T. & A.D. Poyser, London, pp. 350-363.
- Harris M.P., Wanless S., Rothery P., Swann R.L., Jardine D., 2000, Survival of adults common guillemot *Uria aalge* at three Scottish colonies. Bird Study 47, 1-7.
- Hedrick P.W., 1999, Population Genetics. Jones and Bartlett, Boston, USA. 2nd edition.
- Hedrick P.W., 2001, Conservation genetics: where are we now? Trends Ecol. Evol. 16, 629-636.
- Heubeck M., Camphuysen K., Bao Casal R., Humple D., Sandoval Rey A., Cadiou B., Bräger S., Thomas T., 2003, Assessing the impact of major oil spill on seabird populations. Mar. Pollut. Bull. 46, 900-902.
- Hobson K.A., 1999, Tracing origins and migration of wildlife using stable isotopes: a review. Oecologia 120, 314-326.
- Hope Jones P., 1984, Skins of guillemots *Uria aalge* and razorbills *Alca torda* examined at Cascais, Portugal, in May 1982. Mem. Mus. Mar. Portugal 3 (27), 1-10.
- Hope Jones P., 1988, The European cline in wing-length of guillemots *Uria aalge*. Seabird 11, 19-21.
- Hope Jones P., Blake B.F., Anker-Nilssen T., Rostad O.W., 1982a, The examination of birds killed in oilspills and other incidents - a manual of suggested procedures. Nature Conservancy Council, Aberdeen.
- Hope Jones P., Monnat J.-Y., Harris M.P., 1982b, Origins, age and sex of auks (Alcidae) billed in the 'Amoco Cadiz' oiling incident in Brittany, March 1978. Seabird Rep. 6, 122-130.
- Hudson P.J., 1985, Population Parameters for the Atlantic Alcidae. In: Nettleship D.N., Birdhead T.R. (Eds.), The Atlantic Alcidae. Academic Press, London, pp. 233-261.
- Ibarguchi G., Birt T.P., Warheit K.I., Boag P.T., Friesen V.L., 2000, Microsatellite loci from common and thick-billed murre, *Uria aalge* and *Uria lomvia*. Mol. Ecol. 9, 638-639.
- Kampp K., Falk K., 1998, A long distance colony shift by a thick-billed murre. Colon. Waterbird 21, 91-93.
- Lott C.A., Meehan T.D., Heath J.A., 2003, Estimating the latitudinal origins of migratory birds using hydrogen and sulphur stable isotopes in feathers: influence of marine prey base. Oecologia 134, 505-510.
- Lyngs P., 1993, Colony interchange in Baltic Guillemots *Uria aalge*. Dansk Orn. Foren. Tidsskr 87, 247-250.
- Mavor R.A., Parsons M., Heubeck M., Pickerell G., Schmitt S., 2003, Seabird numbers and breeding success in Britain and Ireland, 2002. Joint Nature Conservation Committee, Peterborough, UK Nature Conservation, No. 27.
- Møller A.P., Erritzøe J., 2001, Dispersal, vaccination and regression of immune defence organs. Ecol. Lett. 4, 484-490.

- Moum T., Erikstad K.E., Bjorkild E., 1991, Restriction fragment analysis of mitochondrial DNA in Common Murres, *Uria aalge*, from four Norwegian seabird colonies. *Can. J. Zool.* 69, 1577-1584.
- Moum T., Arnason E., 2001, Genetic diversity and population history of two related seabird species based on mitochondrial DNA control region sequences. *Mol. Ecol.* 10, 2463-2478.
- Nettleship D.N., Evans P.G.H., 1985, Distribution and Status of the Atlantic Alcidae. In: Nettleship, D.N., Birdhead T.R. (Eds.), *The Atlantic Alcidae*. Academic Press, London, pp. 53-154.
- Piatt J.F., Lensink C.J., 1998, *Exxon Valdez* bird toll. *Nature* 242, 865-866.
- Pethon P., 1967, The systematic position of the Norwegian common murre (*Uria aalge*) and puffin (*Fratercula arctica*). *Nytt Mag. Zool.* 14, 84-95.
- Russell R.W., 1999, Comparative demography and life history tactics of seabirds: implications for conservation and marine monitoring. *Am. Fish. Soc. Symp.* 23, 51-76.
- Seip K.L., Sandersen E., Mehlum F., Ryssdal J., 1991, Damages to seabirds from oil spills: comparing simulation results and vulnerability indexes. *Ecol. Model.* 53, 39-60.
- Slatkin M., 1989, Detecting small amounts of gene flow from phylogenies of alleles. *Genetics* 121, 609-612.
- Swann R.L., Ramsay D.K., 1983, Movements from and age of return to an expanding Scottish guillemot colony. *Bird Study* 30, 207-214.
- Tirard C., Helfenstein F., Danchin E., 2002, Polymorphic microsatellites in the black-legged kittiwake, *Rissa tridactyla*. *Mol. Ecol. Notes* 2, 431-433.
- Tuck L.M., 1960, *Les Marmettes*. Duhamel, Ottawa, Canada.
- Weir D., Kitchener A., McGowan R., Kinder A., Zonfrillo B., 1997, Origins, population structure, pathology and diet of samples of diver and auk casualties of the *Sea Empress* oil spill. CCW *Sea Empress* Contract Report.
- Wernham C.V., Peach W.J., Browne S.J., 1997, Survival rates of rehabilitated guillemots. *BTO Res. Rep.* No. 186.
- Wiens J.A., 1996, Oil, seabirds and science. *BioScience* 46, 587-597.
- Wiens J.A., Crist T.O., Day R.H., Murphy R.H., Hayward G.D., 1996, Effects of the *Exxon Valdez* oil spill on marine bird communities in Prince William Sound, Alaska. *Ecol. Appl.* 6, 828-841.
- Wright S., 1931, Evolution in Mendelian populations. *Genetics* 16, 111-123.