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Potential use of population viability analysis to assess the impact of offshore windfarms on bird populations

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Executive summary

- Offshore windfarms are likely to become one of Europe's most extensive technical interventions in marine habitats. European inshore coastal and offshore marine waters support globally significant numbers of seabirds and the UK Government has legal obligations to monitor the effects coastal developments will have on populations of these species.
- Although conventional impact assessments allow estimates of the number of birds that might collide with or be displaced by windfarms, such methods do not allow the overall effect on bird populations to be established. This report determines whether sufficient demographic information is available to carry out population viability analysis: one method of determining the impacts of offshore windfarms on bird populations.
- We consider the data availability for the following species, which we consider the most likely to be affected by offshore windfarms: red-throated diver (*Gavia stellata*), black-throated diver (*Gavia arctica*), great crested grebe (*Podiceps cristatus*), fulmar (*Fulmarus glacialis*), gannet (*Morus bassanus*), cormorant (*Phalacrocorax carbo*), shag (*Phalacrocorax aristotelis*), eider (*Somateria mollissima*), common scoter (*Melanitta nigra*), velvet scoter (*Melanitta fusca*), arctic skua (*Stercorarius parasiticus*), great skua (*Catharacta skua*), little gull (*Larus minutus*), black-headed, gull (*Larus ridibundus*), common gull (*Larus canus*), lesser black-backed gull (*Larus fuscus*), herring gull (*Larus argentatus*), great black-backed gull (*Larus marinus*), kittiwake (*Rissa tridactyla*), sandwich tern (*Sterna sandvicensis*), arctic tern (*Sterna paradisaea*), little tern (*Sternula albifrons*), guillemot (*Uria aalge*), razorbill (*Alca torda*) and puffin (*Fratercula arctica*).
- For most species likely to be affected by offshore windfarms, sufficient demographic data exist to carry out population viability analyses. There is good information on adult survival for all species with the exception of little tern and little gull. Similarly, for all species except little gull, there is good information on productivity. Reasonable data on age-dependent survival and productivity and on the proportion of non-breeders and inter-colony movements are available for about half of the species assessed.
- However, there are some limitations with regards to what population viability analysis can achieve. Mortality resulting from windfarms may reduce competition for resources, thus reducing the rate of natural mortality. The extent of the latter cannot be determined solely through conventional population viability analysis, but also requires detailed understanding of the extent to which demographic parameters are density-dependent. Reasonable data on density-dependence are only available for three species: cormorant, shag and kittiwake. A summary of data availability is given in Table 2 (click here).
- Nevertheless, population viability analysis provides a robust framework for taking a scenarios-based approach in which likely impacts are determined using upper- and lower-bound estimates of unknowns. As such, best-case and worse-case scenarios could be determined.

Glossary

Confidence Interval - if one is not certain about a value such as the number of eggs laid by a bird, because that value is prone to variability, one can express the likelihood of it occurring within a specified range of numbers through the use of Confidence Intervals. For example, it may be that on average, a particular bird species lays 3 eggs each year, but sometimes they lay more and sometimes less. Specifying 95% Confidence Intervals of 2 and 5 say, (95% CI = 2-5), suggests that one can be 95% certain that a bird of that species will lay between 2 and 5 eggs, or put another way, 95% of birds of that species lay between 2 and 5 eggs.

Demographic parameter – any one of the factors, such as adult survival, fledgling, number of eggs laid etc. that affect population growth and hence, population size and viability.

Density-dependence – used in the context of this report to indicate that the value of one or more of the demographic parameters (survival productivity etc.) is dependent upon how many birds are present within a given area or population. For e.g. more birds leads to increased competition, fewer birds leads to reduced competition for resources.

Metapopulation - consists of a group of spatially separated populations of the same species which interact at some level, usually in that individuals regularly travel between the separated populations.

Monte-Carlo simulations – are a widely used class of computational algorithm for simulating the behaviour of various physical or mathematical systems. The process typically involves generating random datasets that have the same characteristics (e.g. mean, variance, mathematical distribution) as real data, repeatedly analysing these randomly generated datasets as one would real data and then quantifying the proportion of times a specified result is obtained.

Population dynamics - the study of changes in the numbers, individual weights and / or age composition of individuals in one or several populations, and biological and environmental processes influencing those changes.

Population viability – the probability that any given population will persists over a specified time period.

Population viability analysis – the process of determining the probability that a population will persist over a specified time period. Population viability models differ from other (deterministic) models in that stochasticity is accounted for.

Pulli – young birds that have typically not left the nest yet or not yet independent of adult.

Standard error (SE) – a measure of the variability in any given set of values or numbers. In instances where the probability distribution (the spread of the numbers around the mean) of these numbers is known, they can be used to calculate an exact Confidence Interval. If all numbers occur with equal probability the standard error can be calculated by square-rooting the average of the squared differences between each of the numbers and the mean of the numbers and then dividing this by the square root of the total number of values in the dataset.

Stochastic event –an event which occurs by chance, used in the context of this report to refer to random events such as a severe storm which may have an impact on one or more of the demographic parameters.

Wreck – in the context of this report, used to describe an event where a large number of seabirds are driven, exhausted onshore by severe weather and experience adverse feeding conditions. The birds are often in poor condition and experience higher than usual rates of mortality.

Acronyms

BTO – British Trust for Ornithology

CEH – Centre for Ecology and Hydrology

COWRIE – Collaborative Offshore Wind Research Into the Environment

GAPPS – Generalized Animal Population Projection System (software used to perform PVAs)

GB – Great Britain

PVA – Population Viability Analysis

RAMAS - Risk Analysis and Management Alternatives Software (software used to perform PVAs)

UK – United Kingdom

ULM – Unified Life Models (software used to perform PVAs)

1. Introduction

The UK government is committed to obtaining 10% and 20% of the UK's electricity from renewable sources by 2010 and 2020 respectively. Suitable land locations have become very limited and consequently major plans for offshore windfarms have been announced (Innogy 2003). According to current plans, within about 10 years, windfarms with a combined output of 40,000 megawatts will be installed in European seas, requiring an area of about 13,000 km^2 (Exo *et al.* 2003; Wind Directions 2003). Offshore windfarms are likely to become one of Europe's most extensive technical interventions in marine habitats (Merck and von Nordheim 2002; Exo *et al.* 2003).

Offshore windfarms can potentially have detrimental effects on the environment. One such effect is on the seabirds and waterbirds (swans, geese, ducks, divers, auks, gulls and terns) that are found offshore. Mortality rates for some species of seabird, seaduck and geese may increase due to collision with or displacement from windfarm turbines. In the UK, all wild birds have a level of protection under the 1981 Wildlife and Countryside Act. Additionally, European inshore coastal and offshore marine waters support globally significant numbers of seabirds (Carter *et al.* 1993, Skov *et al*. 1995) and European Union Member States are obliged to protect populations of these species, under the EU Directive on the Conservation of Wild Birds (79/409/EEC, the Birds Directive) and the Ramsar Convention on Wetlands (Ramsar Convention Bureau 1988). These international agreements, together with the United Nations law of the Seas (United Nations 1982) and the EU Directive on the Assessment of the Effects of Certain Plans and Programmes on the Environment (2001/42/EC, the SEA Directive) require that states accept responsibility for assessing the effects of major offshore development on the environment. Governments are thus legally obliged to determine the impact such developments would have on bird populations.

However, even if windfarms have a high impact on individuals of a bird population by, for example, resulting in a high number of mortalities due to collisions, the impact of windfarms on bird populations as a whole might be negligible, particularly if the mortality is compensated for by sufficiently high rates of birth into the population. Alternatively, population growth rate and possibly population viability could decrease. Population modelling could be used to help evaluate the consequences of changes in mortality rates on population growth rates and population viability. The intended purpose of this report is to use a combination of literature review and interpretation to assess whether sufficient information exists to carry out robust population viability analyses for the species of waterbird and seabird known or thought to be affected by offshore windfarms. Ecologists regularly describe population changes via simple, discrete-time matrix models (e.g. Caswell 2000). These require reliable estimates of demographic parameters such as survival and fecundity, obtained from field data. Population viability analysis (PVA) is the adoption of such models to predict the future continuation or "viability" of the population in question, taking into account stochastic events. A range of different ecological scenarios might be considered, and software for performing the analyses is widely available (*e.g.* Harris *et al.* 1996; Lacy 1993; Legendre and Clobert 1995; Akçakaya 2003).

It is worth bearing in mind however, that population viability analysis, or indeed any population modelling only goes part way to addressing the impact of windfarms on bird populations. It can only determine the impact on the population if the extent to which windfarm induced mortality is additional to other known causes of mortality. Mortality resulting from any one factor may reduce competition for resources amongst remaining individuals, thus reducing the rate of natural mortality. The extent of the latter cannot be determined solely through conventional population viability analysis, but also requires detailed understanding of the extent to which demographic parameters are density-dependent. This issue is discussed in more detail in various places in the report to highlight the limitations and strengths of population viability analysis more specifically.

2. Population viability analysis

2.1 Background

Population viability analysis (PVA) is a species-specific process used to identifying the process that determines the probability that a population will go extinct within a given number of years (Shaffer, 1983; 1987; Boyce 1992) and is thus used to identify the most important threats facing a particular species population. It differs from conventional population modelling in that it takes into account stochastic events, i.e. random changes in demographic rates such as survival or productivity. As such, it is the variability in demographic parameters that is as important as mean values and the greater the variability, the more prone a population is to extinction all other things being equal. Population viability analysis is often oriented towards the conservation and management of rare and threatened species, with the goal of applying the principles of population ecology to improve their chances of survival. Threatened species management has two broad objectives. The short-term objective is to minimize the risk of extinction. The longer-term objective is to promote conditions in which species retain their potential for evolutionary change without intensive management. PVAs are often used to reveal the sensitivity of populations to particular demographic parameters so that the most important impacts on extinction probabilities can be determined. Extrinsic forces, such as habitat loss, over-harvesting, and competition or predation by introduced species, often lead to population decline. Although the traditional methods of wildlife ecology can reveal such deterministic trends, random fluctuations that increase as populations become smaller can lead to extinction even of populations that have, on average, positive population growth when below carrying capacity and mechanisms that incorporate intrinsic factors are needed if extinction risks are to be determined (Lacy 1993).

PVAs can be used to address several questions, and often the nature of these changes during the course of a PVA analysis as the process is refined. Typically, initial questions are very general, such as "Is this species threatened, and if so, why?" PVAs often then concentrate on the identification of factors (including natural factors and human impacts) that are important in dynamics of the specific populations and meta-populations under study, as well as conservation and management options. The methods to be used for this depend on the specific case at hand, and might include statistical analysis of historical data, comparison of populations that are declining with those that are stable, and correlating recent changes in the environment (climatic or habitat changes, introduced species, changing harvest patterns, etc.) with changes in the species. In the context of this report, the broad question is “do offshore windfarms have a deleterious effect on bird populations?” Specific questions are likely to be “what is the maximum level of windfarm-induced mortality that can be absorbed by bird populations of species X, so that the overall population does not decline by an amount greater than Y within Z years” or “given that windfarms cause X number of bird species Y to die, by how much will the population decline within Z number of years?”

2.2 Model structure and data requirements

The model structure for a PVA is primarily determined by the question at hand, the available data, and important characteristics of the species, such as complex social structures or age of first reproduction. Scientists usually incorporate stochasticity, i.e. random variability over time into the model in some way. Model selection is important: an overly complicated model can reduce precision, while an overly simple model may not be accurate. Before settling on a particular PVA model, it is best to examine a few potential models to gain understanding of the effects of different model structures on results. However all PVAs use as their basis, a simple matrix population model (Caswell 2000) in which populations are modelled using the following basic equation:

$$N_{(t+1)} = N_t + B - D + I - E$$

where, $N_{(t+1)}$ is the abundance at time t +1, N_t is the abundance at time t, B is the number of births within the population between N_t and $N_{(t+1)}$, D is the number of deaths within the population between N_t and $N_{(t+1)}$, I is the number of individuals immigrating into the population between N_t and $N_{(t+1)}$ and E is the number of individuals emigrating from the population between N_t and $N_{(t+1)}$. Although this equation is inherently simple, estimation of each of the parameters is more complex and often requires subdivision of these parameters into further components or the use of proxy methods to estimate them. For example, estimates of B might be obtained via a ratio of young to adults soon after the breeding season, or estimates of D via mortality rates of adults and immatures accounting for differences in age structure. Often immigration and emigration are ignored because they are so difficult to estimate.

The precise parameters requiring estimation will depend on the model structure, and for most PVA studies, data are insufficient and a range of numbers is used for some parameters instead of a single number. These ranges can be used in a sensitivity analysis: models are run many times, with different combinations of the low and high values of each parameter to make sure that all uncertainty in parameter values is accounted for. This provides a way to measure the sensitivity of results to each parameter. Sensitivity analysis is useful for determining which parameters need to be estimated more carefully. In most cases, models also include random variation (stochasticity), which necessitates that the results are presented in probabilistic terms, i.e., in terms of risks, probabilities or likelihoods.

In the context of seabirds, demographic parameters often vary spatially and temporally in relation to variability in resource availability. As a result of this, incorporation of stochastic processes into the modelling process is likely to be useful at least in so far as some measure of this variability is incorporated. Many seabird species are long-lived and only attain reproductive age after several years and survival varies with age. Consequently there is a need to account for the age-structure of populations and derive separate estimates of birth and death rates for several age-classes.

2.3 Computer software

Several software packages are available for performing population viability analysis. Five of the most widely used are GAPPS (Harris *et al.* 1986), INMAT (Mills and Smouse 1994), RAMAS (various versions, e.g. Ferson and Akçakaya 1990; Ferson 1994; Akçakaya 1996; 2006; Akçakaya *et al.* 2003), VORTEX (Lacy 1993) and ULM (Legendre and Clobert 1995).

All the software packages normally model population processes as discrete, sequential events using matrix model algebra. Outcomes are assumed to be probabilistic and birth and death processes and the number of progeny produced by each female are simulated by generating random numbers with a specified mean and variance. However, the packages differ in the extent to which more complex procedures can be modelled. For example although all the software packages allow incorporation of age (or stage) structure, VORTEX assumes that fecundity is independent of age after an animal reaches reproductive age (Lacy 1993). Similarly, although all allow density-dependence to be modelled to some extent, VORTEX only accounts for this by imposing a carrying-capacity by a probabilistic truncation of each age class if the population size exceeds the specified carrying capacity (Lacy 1993). Only ULM enables density-dependent processes to be modelled in a sophisticated manner. Similarly, although VORTEX, GAPPS, INMAT and ULM allow inbreeding-depression to be modelled by decreasing the viability of inbred animals, RAMAS does not (Legendre and Clobert 1995; Brook *et al.* 1999). Systematic pressures such as habitat decline can be modelled using RAMAS, ULM or VORTEX, but not using GAPPS or INMAT. Using GAPPS, RAMAS, VORTEX and ULM it is possible to model catastrophes defined according to a specified impact (a fractional multiplier on survivorship), but not using INMAT. A comparative list of the capabilities of each software package is given in Table 1.

Table 1. Comparative capabilities of various PVA software packages

FACTOR	**GAPPS**	**INMAT**	**RAMAS**	**ULM**	**VORTEX**
Age-dependent survival	Y	Y	Y	Y	Y
Age-dependent productivity	Y	Y	Y	Y	L
Catastrophic events	Y	N	Y	Y	Y
Demographic stochasticity	Y	Y	Y	Y	Y
Density-dependence migration	N	N	N	Y	N
Density-dependence productivity	N	N	N	Y	N
Density-dependent recruitment	N	N	N	Y	Y
Density-dependent survival	L	L	L	Y	L
Inbreeding depression	Y	Y	N	Y	Y
Meta-population structure	Y	N	Y	L	Y
Spatial data incorporation	N	N	Y	L	L
Systematic pressures	N	N	Y	Y	N

Y=Yes, N=No, L=Limited

Overall it appears that ULM performs best for the types of PVAs most appropriate for seabirds.

3. Demographic data availability

3.1 Interpretation of species accounts

We present demographic information on the 16 species we consider to be the most vulnerable to colliding with wind turbines or to being displaced from offshore windfarm areas. The selection of species is based primarily on the vulnerability index developed by Garthe and Hüppop (2004). However a greater emphasis has been placed on species associated with UK coastal and marine areas and on species identified as particularly vulnerable in environmental scoping, baseline and impact assessments or environmental statements for offshore windfarms in UK waters (e.g. GREP UK Ltd 2002; Hydrosearch 2002; Innogy 2003; Banks *et al.* 2005, 2006, 2007; Maclean *et al.* 2007). Selection is also based on the COWRIE Birds sub-group and the authors' expert knowledge of seabird distributions and ecology.

We have included as much information as was possible within the prescribed timeframe available to carry out background research for this report, but it is possible that not all available sources have been identified. We used ISI Web of Knowledge (isiknowledge.com) to find relevant literature, typing in the Latin binomial of each species into the search engine and searching the title, keywords and abstract. The title abstract of all literature returned by the search engine was then read to determine whether relevant, and for key references, the entire article was obtained. We also searched every issue of several of the more relevant but obscure journals, such as Atlantic Seabirds, which are not held within the Web of Knowledge database. Additional information was obtained from secondary literature sources such as Glutz von Blotzheim & Bauer (1982), Lack (1986), del Hoyo *et al.* (1992 and 1996), Gibbons *et al.* (1993), Wernham *et al.* (2002), Mitchell *et al.* (2004) and Mavor *et al.* (2006). Although emphasis is placed on detailing results from studies that examine those breeding or wintering populations likely to be found in UK inshore and offshore waters, details from studies conducted elsewhere are also included. To facilitate interpretation, a brief overview of the distribution and broad migratory patterns of UK breeding and wintering populations is given at the start of each species account.

To fully quantify the dynamics of populations and thus apply population viability analysis, it is not only necessary to quantify individual demographic parameters, but also to understand the intrinsic and extrinsic factors that affect these. This information is essential for two reasons: (1) because it indicates the likely variability in individual parameter variables, which must be known for population viability analyses to be performed and (2) because intrinsic and extrinsic factors interact with each other. Thus, if windfarms cause mortality, but it is generally known that population sizes are limited by food viability, windfarm induced mortality may be compensated for by a reduction in competition for food. That said, it is worth considering that for many long-lived species, adult mortality can result in recruitment of younger birds to the population leading to an overall long-term decline in the population even if the actual number of breeders remains stable.

For almost all species, the most important intrinsic factors are age and/or experience, which can affect survival, breeding productivity and dispersal, in the case of the former two, usually unimodally with a steady increase as the bird ages, but a sharp decrease as the bird reaches old-age. Extrinsic factors include predation or any other factor which causes mortality and resource availability, such as the availability of food. Many studies have examined demographic parameters in relation to such factors and where possible details of these factors are given in the species accounts. When interpreting the species accounts, it is also worth bearing in mind that long-term studies and/or those which span several locations are likely to give more reliable demographic parameter values and give a better picture of the inherent variability in these.

3.2 Red-throated diver (*Gavia stellata*)

The majority of red-throated divers occur offshore during the winter period. Baker *et al.* (2006) suggest that 4,850 red-throated divers winter in GB inshore and near off-shore waters, although the discovery of a sizable over-wintering population in the Outer Thames Estuary as part of the DTI (now BERR) aerial survey protocol, has prompted estimates of c. 17,000 birds (O'Brien *et al.* in press). This population comprises birds from the UK breeding population (the majority of which is on Shetland), supplemented by numbers from Scandinavia and a smaller number from Greenland (Lack 1986; Wernham *et al.* 1993).

There are some survival estimates. Adult survivorship is listed as 0.84 in Garthe and Hüppop (2004), which is derived from Hemmingson and Ericson (2002). No variability measures are given in the former. Pre-fledging survivorship rates of birds in Canada are given in Douglas and Reimchen (1988).

There is better information on reproductive success and breeding productivity. The number of pairs and the number of birds fledged per pair during 2004, 2005 and between 1986 and 2004 (means and standard errors) is given for 11 localities in the British Isles in Mavor *et al.* (2006). The breeding performance of red-throated divers in Shetland is given in Gomersall (1986) and breeding success in southern Finland in Lokki and Eflök (1984). Reproductive success of red-throated divers in North America in relation to distance of the nest from the ocean, is given in (Eberl and Picman 1993) and breeding productivity of birds in Canada in Dickson (1993). It is likely that the breeding success of birds in North America will be indicative of that in Greenland, from where some of the UK over-wintering population originates. Data on immature survivorship, age of first breeding, the proportion of non-breeders and migration between populations are lacking.

3.3 Black-throated diver (*Gavia arctica*)

The majority of black-throated divers occur offshore during the winter period. Baker *et al.* (2006) suggests that 700 black-throated divers over-winter in GB inshore and near off-shore waters. This population probably consists of birds from the UK breeding population, supplemented, particularly in the south-west, by birds of Scandinavian origin (Lack 1986).

There are some survival estimates. Garthe and Huppop (2004) list adult survivorship as 0.85, which is derived from Nilsson (1977) and Hemmingson and Ericson (2002). No variability measures are given in the former, but the original data provides some information on changes in these values. Nilsson (1979) lists adult survivorship as 0.89, with minimum 95% confidence limits of 0.87 and 0.91, based on 76 published long-distance recoveries of birds ringed on spring migration in the south-eastern Baltic. Pre-fledging survival estimates are given in several of the studies in which breeding productivity is estimated (see next paragraph).

There are more widespread estimates of the various components of breeding productivity. In southwest Sweden, the average reproduction was 0.40 half-grown, fledged young per pair per year, similar to other areas in south Sweden (Andersson *et al.* 1980) and Finland (Parkarinen 1989), and close to the minimum of 0.4-0.5 fledged young per pair which Nilsson (1977) estimated to be necessary for the maintenance of a stable population (Eriksson 1994). In Scotland, the mean number of chicks fledged per nest that hatched was 0.95 at lakes where three-spined sticklebacks *Gasterosteus aculeatus* and/or minnows *Phoxinus phoxinus* were present and 0.64 where they were absent, with chick survival also positively related to June temperature and the abundance of fish in lakes with fish present, but inversely related to sunshine duration in June (Jackson 2005). In Fegen-Svansjarna (Sweden) and south-west Sweden, the mean breeding success was 0.44 and 0.38 chicks per pair each year respectively. There are also estimates from Scotland, suggesting that productivity is geographically variable. In west Sutherland overall breeding success is low averaging 0.23 chicks per territorial pair per year, while in Ross-shire it was 0.29 (Mudge and Talbot 1993). Breeding success is highly dependent upon fluctuations in water-level both in Scotland (Mudge and Talbot 1993) and Scandinavia (Hake *et al.* 2005), but is also dependent on food availability (Eriksson 1986). In Scotland, the provision of artificial floating islands for nesting Black-throated Divers improved chick productivity by a factor of 2.7 and probably improved chick production of the Scottish black-throated diver population by 44% (Hancock 2000). Data on immature survival, age of first breeding, the proportion of non-breeders and migration between populations are lacking.

3.4 Great crested grebe (*Podiceps cristatus*)

The majority of great crested grebes occur offshore during the winter period. Baker *et al.* (2006) estimates that c. 19,140 over-winter in the UK, but only a small proportion, dependent upon weather conditions, do so in UK inshore and near off-shore waters. About half of these are UK breeders, and the remainder probably originate from continental Europe, including Denmark (Lack 1986, Wernham *et al.* 2002). Indeed, the total number over-wintering in the UK is often higher during extended periods of cold weather on the continent (Lack 1986).

There is some information of survival rates. Adult survivorship is listed as 0.7 in Garthe and Hüppop (2004), which is derived from Fuchs' (1982) analysis of ringing-recoveries in Germany. Some details of chick survival in relation to prey availability in the Netherlands are given in Ulenaers and Dhondt (1991 and 1994). Chick mortality has been shown to be affected by parental fishing and is generally highest in the first two weeks of life. Amongst chicks younger than 3 weeks old, the rate of biomass intake per brood was correlated with the estimated prey abundance. Some details of nest survival in Finland are given in Ulfvens (1988). Some details of clutch sizes in Poland, particularly in relation to coloniality and nest-site characteristics are given in Bukacinska *et al.* (1993).

There is limited information on breeding productivity available from Robertson (2005), which lists typical clutch sizes and age of breeding, but little else. Immature survival, age of breeding, the proportion of non-breeders and migration populations are lacking.

3.5 Fulmar (*Fulmaris glacialis*)

Fulmars occur offshore throughout the year. Baker *et al.* (2006) estimate the UK breeding population to be just over half a million pairs, which is derived from Mitchell *et al.* (2004), but no over-wintering estimate is provided. The majority of breeders, according to Lack (1986), disperse fairly locally into onshore and near-offshore waters during winter, although there is evidence of more widespread dispersal, with birds ringed as pulli in the UK recovered from as far away as Newfoundland, Greenland, Spain and Russia (Wernham *et al.* 2002).

There is fairly good information on survivorship. Adult survivorship is known to be very high, listed as 0.986 in Garthe and Hüppop (2004), which is based on figures reported in del Hoyo *et al.* (1992), with further estimates given in Dunnet and Ollason (1978a) and Ollason and Dunnet (1983), the former of which also provides comprehensive details of survival within different age classes. Chick survival on Fair Isle is given in Gray *et al.* (2003) and appears to be affected by sandeel *Ammodytes marinus* availability, with lower breeding success recorded in years with few sandeels. A brief summary of the literature describing survival in relation to age is given in Mitchell *et al.* (2004). There is also some information on age of first breeding (9.2 ± 0.6 S.E.) and natal dispersal: 90% of birds surviving breeding age, move away from their natal colony (Dunnet and Ollason 1978b). Mitchell *et al.* (2004), also give details of the proportion of non-breeders, again derived from other sources.

There is also good information on reproductive success. The number of pairs and the number of birds fledged per pair during 2004, 2005 and between 1986 and 2004 (means and standard errors) is given for 35 localities in the British Isles in Mavor *et al.* (2006). In north-eastern Greenland, overall breeding success (chicks fledged per egg laid) was 0.56, with hatching success being negatively correlated with laying date and the proportion of egg neglected, while overall breeding success was correlated negatively with distance to nearest neighbouring site and positively with the length of the chick-guard period (Falk and Mollers 1997). As such, measures of variability in the data are also provided. Fledging success is highly dependent upon parental experience. Although the breeding success of younger birds (< 9 years old) is similar to that of older birds (> 9 years old) at 0.36 and 0.37 respectively, older birds fledge 0.83 of their chicks compared with only 0.25 in the younger birds, resulting in overall breeding successes of 0.31 and 0.09 young per egg, respectively. Some measures of variability are also given in this study. Further details of fulmar breeding parameters are given in Dunnet *et al.* (1979). Some details of the relative effects of parental performance and egg quality on breeding success are given in Ollason and Dunnet (1986). Thompson and Walsh (2000) provide information on breeding success between 1978 and 1998 on Orkney. Detailed information on migration between colonies is lacking however, as is direct information on the proportion of non-breeders within the population as a whole.

3.6 Gannet (*Morus bassanus*)

Gannets occur offshore throughout the year. Baker *et al.* (2006) estimate the UK breeding population of gannets (number of nests) to be 218,546, which is derived from Mitchell *et al.* (2004), but no winter estimate is provided. After fledging, most young migrate southwards during August and September, down the Atlantic seaboard, through Biscay, to tropical waters of West Africa (Lack 1986). A few spend their first winter in UK waters, but only 1-2% of birds seen in winter have immature plumage (Lack 1986). It is thought that most breeding adults remain, highly dispersed, in UK waters, but some certainly move south to warmer waters (Lack 1986), with the majority of ringing recoveries from France, Spain, Portugal and West Africa, but also some from Scandinavia and the Mediterranean (Wernham *et al.* 2002). Second to fourth year birds also disperse, mainly southwards, with a decreasing proportion doing so with age (Wernham *et al.* 2002).

There is reasonable information on survival. Adult survivorship is listed as 0.94 in Garthe and Hüppop (2004), which is based on figures reported in del Hoyo *et al.* (1992). No variability measures are given in the former. Wanless *et al.* (2006) estimate mean annual survival of adult gannets to be 0.916 on the Bass Rock and 0.922 on other colonies in Britain and Ireland, with annual survival over the first four years of life increased gradually from 0.424 to 0.895 before reaching this adult value. Some measures of variability are also given. Prior to maturity there were differences between the survival probabilities of chicks ringed on the Bass Rock and those ringed elsewhere, but for both groups survival to age four years was about 0.30 (Wanless *et al.* 1996). Further estimates of age-dependent mortality at the Bass Rock colony are given in Nelson (1966), where it is also stated that gannets invariably lay one egg.

There is fairly good information on breeding productivity. The number of pairs and the number of birds fledged per pair during 2004, 2005 and between 1986 and 2004 (means and standard errors) is given for 6 localities in the British Isles in Mavor *et al.* (2006). Mitchell *et al.* (2004) gives a brief overview of the literature detailing information on the proportion of non-breeders.

3.7 Cormorant (*Phalocrocorax carbo*)

Baker *et al.* (2006), estimate the UK breeding population to comprise 9,018 pairs and the over-wintering population to consist of 24,300 individuals, with an increasing number of the continental race *P. c. sinensis* now over-wintering in the UK (Newson *et al.* 2005). However, coastal birds comprise almost entirely of the nominate race (Marion and Le Gentil 2006). Birds disperse fairly widely from breeding grounds, with movements of up to 800 km in the first winter, typically from continental Europe (Lack 1986; Wernham *et al.* 2002).

There is reasonable information on survivorship, although much of this is for the continental race. Adult survivorship is listed as 0.84 in Garthe and Hüppop (2004), which is based on figures reported in Krementz *et al.* (1989), the latter of which provides information on variability, even though the former does not. An example of the use of bird ringing to estimate survival is given in Lebreton (2001). Two studies make use of the same data as in Lebreton (2001) to determine density-dependent impacts on survival in *sinensis*: Frederiksen *et al.* (2001) and Frederiksen and Bregnballe (2000). However, a long-term study has also used ringing recoveries to monitor long-term survival rates of adult and first-year British and Irish cormorants (Wernham and Peach 1999), the majority of which belong to the nominate race. Budworth *et al.* (2000) provide information on survivorship of the nominate race in Caithness in Scotland. Mitchell *et al.* (2004) gives a good overview of the literature on survivorship of the nominate race. There are some details of dispersal from and recruitment to a colony in Denmark given in Henaux *et al.* (2007). Frederiksen and Bregnballe (2001) provide information on age of first breeding.

There is also good information on reproductive success, although again much of this information refers to the continental race *sinensis*. However, the number of pairs and the number of birds fledged per pair during 2004, 2005 and between 1986 and 2004 (means and standard errors) is given for 7 localities in the British Isles in Mavor *et al.* (2006) all of which, being coastal, are likely to refer to the nominate race. Some details regarding effects of distance breeding area is from wintering area on breeding performance of a colony in Denmark are given in Bregnballe *et al.* (2006), which also gives details of age-related fledging success. Although mean fledgling production per individual did not decrease with increasing distance to the wintering area, lifetime reproductive success of males wintering at intermediate distances from breeding areas was lower than among males wintering closer to or further from the colony. Details of reproductive success and how this effects recruitment at this colony are given in Frederiksen and Bregnballe (2001). In a newly established colony in Italy hatching success was 72-91% and total nesting success, 67-86%, with the number of young fledged per successful nest ranging between 2.3 and 2.9 (Volponi 1999). In the Netherlands, breeding success was influenced by contaminates, with reproductive success (number of young fledged per pair) varying from 0.5 at sites contaminated by DDE and PCBs, to 1.2-1.7 at sites with lower contamination (Boudewijn and Dirksen 1995; Dirksen *et al.* 1995). Breeding success in the Netherlands has also been examined in relation to foraging behaviour (van Eerden 1988). There are also details of breeding performance (clutch and brood size and egg and nestling survival) of the race *carbo.* Details of breeding performance of inland and coastal breeding cormorants in England and Wales are given in Newson *et al.* (2005). Breeding performance was higher at inland colonies because of higher nestling survival during the later stages of nestling development, from 15-56 days, suggesting that demographic parameter values of the two races cannot be used inter-changeably. Information on migration between populations is lacking however, as is information on the proportion of non-breeders. Budworth *et al.* (2000) provide information on breeding productivity of the nominate race in Caithness in Scotland. Andrews and Day (1999) provide information on reproductive success of *carbo* in relation to colony nest position and timing of nesting. Mitchell *et al.* (2004) gives a brief overview of the literature detailing information breeding success. Budworth *et al.* (2000) provide some information on inter-colony movements in Scotland.

3.8 Shag (*Phalocrocorax aristotelis*)

Baker *et al.* (2006) estimate the UK breeding population of shags to comprise of 27,477 pairs, which is derived from Mitchell *et al.* (2004), but no over-wintering estimate is provided. Shags undergo limited movement, and as a consequence over-wintering numbers and distribution are similar to the breeding population (Lack 1986). Very few British or Irish shags leave the country in winter and there is little evidence of birds arriving from the continent (Lack 1986), with the handful of ringing recoveries of birds ringed in the UK found abroad, generally being from nearby coasts (Wernham *et al.* 2002).

There is fairly good information on survival. A detailed long-term study of shags on the Isle of May has provided information on post-fledging survival to three years of 25 cohorts. Mean survival for 10 years was 0.307 ± 0.2 (Harris *et al.* 1994a), and mean annual adults survival for the period 1967-1992 was estimated at 0.878 (95% C.I. = 0.859, 0.897) (Harris *et al.* 1994b). Harris *et al.* (2000) provides estimates of adult survival between 1986 and 1996 from the Isle of May. On the Farne Islands, the average survival rate of shags over the first year was estimated to be 0.51 ± 0.12 and that of adults 0.83. After the first year, age did not usually affect adult survival rates (Potts *et al.* 1980). The survival rate of shags varies significantly from year to year, depending on sudden outbursts of mortality in winter, often associated with prolonged onshore gales. Over-winter survival can also be very adversely affected by weather, For example, during a period of prolonged spell of onshore winds on the Isle of May resulted in a wreck of over-wintering adults such that over-winter survival was reduced from the normal 88% to 14.7%, although this affect was age-dependent (Harris *et al.* 1998). There are similar findings for the Farne Islands (Potts *et al.* 1980). There is some information on migration between populations: the influence of eruptive movements, population size and recruitment on the survival and population dynamics of shags are described in Potts (1967a and b). Details of survival rates and recruitment of a population of shags situated at the southern extremities of its range on the Ciés Islands are given in Velando and Friere (2002). This study also provides comparative details of demographic parameters from other locations. Details of immigration and demographic stochasticity in the formation and growth of a new colony of shags in the western Mediterranean is given in Martinez-Abrain *et al.* (2001).

There is also good information on reproductive success. The number of pairs and the number of birds fledged per pair during 2004, 2005 and between 1986 and 2004 (means and standard errors) is given for 19 localities in the British Isles in Mavor *et al.* (2006). On the Isle of May, the mean number of young fledged per pair of shags was in the region of 1.5, but varied from 0.9 to 1.95, dependent upon conditions and the experience of pairs (Harris *et al.* 1994b). Daunt *et al.* (2007) provide indirect evidence that older and wiser shags on the Isle of May forage better and are thus more likely to have higher breeding success, although no direct measurements of breeding success were undertaken in this study. Potts *et al.* (1980) provide details of the population-dynamics and breeding success of shags on the Farne Islands. Clutch size on the Farne Islands was 3.01 ± 0.04, with hatching success of eggs incubated for the full term at 0.87 ± 0.02. There are also details from colonies in continental Europe. Valando *et al.* (2005) compared reproductive success in colonies affected by and unaffected by an oil-spill in Galicia, Spain. In colonies, unaffected by the oil spill, 2.00 ± 0.08 chicks were fledged per pair, whereas only 0.13 chicks were fledged per pair in the area affected by the spill. Breeding success is also affected by nest site characteristics in this region. Sites where breeding was successful differed from unsuccessful sites with nest-site characteristics especially affected the hatching success (Velando and Freire 2003). Details of reproductive success (young per nest) of a population of shags situated at the southern extremities of its range on the Ciés Islands are given in Velando and Friere (2002). This study also provides comparative details of demographic parameters from other locations. Rindorf *et al.* (2000) examine the effects of sandeel availability in the Danish sandeel fishery on the reproductive output of shags, focusing predominantly on whether breeding success depends on sandeel availability. Velando *et al.* (1999) examines the impact of food limitations on chick mortality, demonstrating that food availability is also reduced by adverse weather. Daunt *et al.* (1999) provides information on age-dependence in breeding success.

There is also some information on between-colony movements: Aebischer (2005) provides information on colony fidelity and inter-colony movements on the east coast of Britain. Detailed information on the proportion of non-breeders within the population is lacking however.

3.9 Eider (*Somateria mollissima*)

Baker *et al.* (2006) estimate the breeding population of eiders in the UK to consist of 31,650 pairs and the over-wintering population to consist of 80,000 individuals. Although the majority over-winter near to their breeding grounds, small numbers are recorded further south in the UK, away from their breeding grounds, which are predominantly in the north (Lack 1986). There are some recoveries of birds ringed in the UK from Scandinavia and vice-versa (Wernham *et al.* 2002).

There is fairly good information on survival, but mostly from non-British populations. Adult survivorship is listed as 0.895 in Garthe and Hüppop (2004), which is based on figures reported in Krementz *et al.* (1997), who investigated the survival in North America. No variability measures are given in the former, but the original data provides some information on changes in these values. Details are also given in Krementz *et al.* (1996) where ringing recovery data are used to estimate the survival of female eiders in North America originating in the Atlantic Coast subpopulation as 0.873 ± 0.0156 (SE). Wilson *et al.* (2007) studied survival of Pacific population of eiders in Alaska and concluded that apparent annual survival of adult eiders is 0.892 (SE = 0.022) and spatially and temporally invariant. However, occasionally mass mortality events can occur, such as the death of 21,000 eiders in the Wadden Sea due to over-exploitation of their main food source: mussels (Camphuysen *et al.* 2002). Some information on nesting and fledging survival is detailed in studies concerned with breeding success, described below.

There is also fairly good information on breeding productivity, although again mainly from non-British populations. Hario and Rintala (2006) investigated the relationship between breeding parameters and population size in Finland, thus providing information on the former. Of the parameters studied, only fledging rate (during a 34-year period) showed a significant negative relationship with population size, indicating density-dependence. Furthermore, the fledging rate responded strongly to the population growth rate and to the rate of recruitment.

Clutch size and duckling (downy young entering the water) rate did not show negative density dependence. Lehikinen *et al.* (2006) demonstrated that breeding success is also influenced by winter climate in the Baltic region. Bolduc *et al.* (2005) showed that nesting success in Canada is influenced by nest site location and female reproductive characteristics, with colonies located on forested islands having higher nesting success than those on open islets. This highlights the potential variability in breeding parameters and demonstrates why information on non-British populations cannot necessarily be extrapolated to British populations without a degree of qualitative interpretation. Mawhinney *et al.* (1999) investigated the productivity of eiders, including duck survival to fledging in the Bay of Fundy in Maine. Christensen (1999) provides information on the effects of cohort and individual variation in duckling body condition on survival and recruitment of eiders in Denmark. Robertson (1995) investigated factors affecting nesting success and Robertson and Cooke (1993) investigated the effects of intra clutch egg-size variation on hatching success of eiders in Hudson Bay, Canada. Swennen (1976 and 1991) investigated fledgling survival and fledgling production by eiders in the Netherlands and Johnson *et al.* (1987) examined reproductive success of the pacific population of eiders, which is at the southern extremities of their breeding range. Conversely, Koryakin *et al.* 1982) investigated the population structure of eiders in northwest Russia, towards the northward extremities of their breeding range.

There are some studies from of UK eider populations. The clutch size of eiders nesting on Coquet Island, Northumberland has been studied for 41 successive years, during which time there has been a progressive decline in the annual mean clutch size, from a peak in 1962 of 5.37 eggs per nest to 3.43 eggs in 1996, indicating some evidence of a density-dependent relationship between clutch size and numbers of adult ducks (Coulson 1999). Some data from Sands of Forvie are also presented in this study. Mendenhall and Milne (1985) assessed the factors determining duckling survival in north-eastern Scotland. Other studies include that conducted by DeVink *et al.* 2005) showing that the survival of ducklings increases with salinity and those conducted by Marshall (1967a, b and c), investigated the effects of nesting densities on clutch size.

There is also some information on age of breeding and migration between populations. Baillie and Milne (1982) determined the effect of female age on breeding in eiders in the UK Chaulk *et al.* (2006) investigated extinction and re-colonisation of eider populations in Canada. Detailed information on migration between populations is lacking however. There is some, but not detailed information on the proportion of non-breeders. Coulson (1984) examined the population dynamics of eiders, demonstrating evidence of extensive non-breeding by adult ducks and but does not give detailed figures.

3.10 Common scoter (*Melanitta nigra*)

Baker *et al.* (2006) estimate the breeding population of common scoters in the UK to comprise 95 pairs, but the over-wintering population to be in the region of 50,000 individuals, the vast majority of which are coastal. The bulk of the wintering population tends to be in major flocks (Lack 1986), making this species especially vulnerable to windfarms, with major concentrations occurring in Carmarthen Bay, Liverpool Bay, the Moray and Dornoch Firths and the Firth of Forth (Lack 1986). Moulting flocks are known to occur at several locations, with high numbers at some locations in late summer, but the main influx takes place in October and November (Lack 1986).

There is some information on survival, but not from UK populations. Adult survivorship is listed as 0.773 in Garthe and Hüppop (2004), which is based on figures reported in Krementz's *et al.* (1997) estimates from North American populations. No variability measures are given in the former, but the original data provides some information on changes in these values. Fox *et al.* (2003) examined the annual survival of breeding females, as determined by capture-recapture of females on the nest in Iceland. Estimated survival over the first year after ringing was 0.749 (95% CI: 0.623-0.843) and annual survival over the following years was 0.783 (0.715 to 0.839). Adult female annual survival is an especially important population parameter in this species, which has a male-biased sex ratio (1.2-2.0 males: 1 female on the breeding grounds).

There is also some information on breeding productivity, but again from non-British populations. Gardarsson and Einarsson (2004) examined the relationship between food availability and the total number of young found at Lake Myvatn in Iceland, with food determining production primarily through availability to young, but with severe weather occasionally having catastrophic effects. Savard and Lamothe (1991) examined aspects of breeding ecology, including duckling mortality of common scoters in Quebec. Information on the proportion of non-breeders, the extent to which survival changes with age and migration between populations is lacking however.

3.11 Velvet scoter (*Melanitta fusca*)

Velvet scoters are a winter visitor to the UK. Baker *et al.* (2006) estimate the UK over-wintering population to comprise 3,000 individuals. Although small numbers can occur almost anywhere on the coast, major concentrations occur in the Moray and Dornoch Firths, in the Firth of Forth and around Orkney (Lack 1986).

There is some information on survival. Adult survivorship is estimated as 0.77 in Garthe and Hüppop (2004), but no variability measures are provided. Krementz *et al.* (1997) examined annual survival rates of velvet scoters at Saskatchewan, Canada and concluded that adult females that winter along both the Pacific and Atlantic coasts, had high annual survival rates (0.73 +/- 0.0176 S.E.). Mikola *et al.* 1994 examined the effects of disturbance caused by boating on survival of velvet scoter ducklings in the archipelago of south-west Finland and determined that broods disturbed more frequently than average were smaller than those disturbed less frequently and that at least 60% of ducklings died before the age of three weeks, predominantly due to predation by herring gulls and great black-backed gulls. Traylor and Alisauskas (2006) examined the influence of intrinsic (physical and nutritional traits of individual females and ducklings, brood sizes) and extrinsic factors (weather, hatching date) on the survival of ducklings in Saskatchewan, Canada. High mortality (c. 0.875) occurred within six days of hatch. Duckling survival probability decreased with advancing hatch date, increased with larger initial brood sizes, was higher for larger, better-conditioned ducklings and increased with favourable weather. Brood survival decreased with advancing hatch date, increased with larger initial brood sizes, and increased with favourable weather. Survival probabilities of ducklings were 0.0061 and 0.0027 in 2000 and 2001 respectively and broods 0.015 and 0.00048, respectively. These figures are lower than any previously reported, possibly due to intense gull predation shortly after hatch.

There is also limited information on breeding productivity. Traylor *et al.* (2004) examined aspects of the nesting ecology of velvet scoters, including Mayfied nest-success estimates (0.35, 95% CI: 0.27, 0.43) in Saskatchewan, Canada. Detailed information on breeding productivity as well as estimates immature survival, the proportion of non-breeders and migration between populations is lacking however.

3.12 Arctic skua (*Stercorarius parasiticus*)

Arctic skuas are a breeding species, but also occur during spring and autumn migration. Baker *et al.* (2006) estimate the UK breeding population to be 2,136 pairs, which is derived from Mitchell *et al.* (2004) but no estimates are given for the migration periods. The main wintering areas include Australia, South Africa and southern South America (Wernham *et al.* 2002). The birds that migrate along the coasts of Britain and Ireland include small numbers that breed in Scotland, but also birds from large populations in the north of Europe (Wernham *et al.* 2002). Spring migration tends to occur further west, with regular spring passage offshore from Sussex, from early April to early June, peaking in early May, while others pass western Ireland and the Western Isles of Scotland. Ringing recoveries suggest that autumn migration occurs down the east coast, with birds most numerous in the North Sea, with UK breeders over-wintering predominantly off southern Africa (Wernham *et al.* 2002), although there are also some recoveries off the coast of Brazil and from inland Sudan and the Congo Basin, the latter two suggesting that some migrate overland (Wernham *et al.* 2002).

There is some information on adult survival. Adult survivorship is listed as 0.84 in Garthe and Hüppop (2004), which is based in figures reported in del Hoyo *et al.* (1996), the latter of which also provides information on variability. Davis *et al.* (2005) examined the effects of supplementary feeding on adult survival and breeding success of arctic skuas in Shetland. The local return rate of adults between seasons, not given supplementary food was about 0.72 ± 0.08 and about 0.91 ± 0.05 for those fed. A few comments on adult survivorship are also given in Mitchell *et al.* (2004). There is also some information on non-breeding. Catry *et al.* (1998) investigated incidences of non-breeding in adults and concluded that only 5.5% of birds (3% of territorial pairs) failed to lay eggs.

There is relatively good information on breeding productivity, particularly in relation to food availability. The number of pairs and the number of birds fledged per pair during 2004, 2005 and between 1986 and 2004 (means and standard errors) is given for seven localities in the British Isles in Mavor *et al.* (2006). Davis *et al.* (2005) examined the effects of supplementary feeding on breeding success of arctic skuas in Shetland. Without supplementary feeding, the number of chicks reared to 20 days per pair is 0.7 ± 0.1 S.E. early in the season and 0.3 ± 0.1 SE later in the season. Phillips *et al.* (1996) examined the influence of food availability on the breeding effort and reproductive success and showed that they are all linked to sandeel availability. Davis (1976) examined the effects of experience on breeding success. Pairs which had bred together for at least two years fledged on average 1.51 ± 0.034 SE chicks, whereas new pairs raised only 0.65 ± 0.066 SE chicks. There is no information on age-dependent survival post fledging and on migration between different populations.

3.13 Great skua (*Catharacta skua*)

Great skuas are a breeding species, but also occur during spring and more numerously during autumn migration. Baker *et al.* (2006) estimate the breeding population to comprise 9,634 pairs, which is derived from Mitchell *et al.* (2004), but no estimates are given for the migration periods. Most UK breeders undergo a comparatively short migration in relation to other skua species, over-wintering off the coasts of southern Europe, prior to returning to the same breeding colonies each year, although immature birds wander more widely accounting for recoveries in South America, the USA, Greenland, Svalbad and northern Russia (Wernham *et al.* 2002). On migration, skuas tend to remain at least 2 km offshore, such that large numbers only occur close to land after strong winds or poor visibility and land-based counts often under-estimate numbers. West coast breeders tend to migrate south directly down the Atlantic coasts of Europe, but those breeding in the Northern Isles, often spend time in the North Sea prior to visiting the Atlantic (Wernham *et al.* 2002). In the UK, peak numbers occur during autumn migration, especially in September in the North Sea, but during October to the west of Britain and Ireland. Avoidance of coasts is such that birds generally do not migrate through the English Channel and autumn migration of great skuas in the North Sea is generally northwards after which birds fly round the north of Scotland on route to the Atlantic. Some Icelandic and Faeroes birds pass the coasts of Britain and Ireland in spring and autumn, however it is generally that that most birds occurring in UK waters on passage also belong to UK breeding populations, as Icelandic birds favour a different migratory route and generally over-winter off the coast of Newfoundland (Wernham *et al.* 2002).

There is fairly good information on survival, albeit predominantly from populations in Shetland. Adult survivorship is listed as 0.90 in Garthe and Hüppop (2004), which is based on figures reported in del Hoyo *et al.* (1996), the latter of which also provides information on variability. Votier *et al.* (2004) examined the survival of great skuas that specialised in depredating other seabirds compared to those feeding predominantly on fish and showed that specialist bird predators showed similar annual survival compared with fish-feeders. Ratcliffe *et al.* (2002) examined the effects of age and year on the survival of breeding adults. Annual survival rates averaged 0.89 but varied among years between 0.82 and 0.93, with annual variations being temporally associated with variations in sandeel abundance during the breeding season. Survival rates of adult great skuas were affected by their age, with survival increasing significantly with age from 0.73 in 5-year-old-birds to between 0.85 and 0.96 in birds from 7 to 22 years old, with a sharp decline to between 0.75 and 0.87 in birds over 22 years old. There is also information on incidence of non-breeding. Catry *et al.* (1998) examined incidences of non-breeding by adults and concluded that 8.9% (range 4-14%) of experienced birds deferred breeding and that higher incidence of non-breeding in great skuas was recorded in years when fledging production was low. Klomp and Furness (1992) and Klomp and Furness (1990) examine incidences of non-breeding on Foula and conclude that it buffers against environmental-stress.

There is also good information on breeding productivity in relation to several factors. The number of pairs and the number of birds fledged per pair during 2004, 2005 and between 1986 and 2004 (means and standard errors) is given for 7 localities in the British Isles in Mavor *et al.* (2006). Furness *et al.* (2006) examined whether winter foraging conditions affected subsequent breeding performance. Votier *et al.* (2004) examined the feeding and reproductive performance of great skuas that specialised in depredating other seabirds compared to those feeding predominantly on fish. In a comparison of reproductive performance, specialist bird predators consistently hatched earlier among years. They also showed larger clutch volumes and improved chick condition, but these were subject to annual variations. Hatching success and fledging success for specialist bird predators and specialist fish predators were similar. Ratcliffe and Furness (1999) examined the effects of experimentally manipulating brood size on the breeding performance of great skuas. Ratcliffe *et al.* (1998a) examined the effects of age and food supply on clutch volumes and hatching success and concluded that although age increases clutch size, up to 18 years, it declines thereafter and food availability had no effect. There was a significant interactive effect between food availability and age on hatching success. Success was uniformly low for birds of all ages in 1988-1990 when sandeel abundance was low. Success increased with age in 1991 and 1992 during which time food supply improved. During 1993 food supply was abundant and fledging success was high in all age classes. A further examination of the effects of age on reproductive success is given in Ratcliffe *et al.* (1998b). All the Ratcliffe studies were carried out on Shetland. Phillips *et al.* (1997) provides a comparison between the reproductive success of birds on St Kilda with those on Shetland. Hamer and Furness (1991) examine age-specific breeding performance in Shetland. (Hamer *et al.* 1991) examine how changes in sandeel availability affect adult territorial attendance and breeding success, which was less than 40% in 1987 and less than 15% in 1988 and 1989. Furness (1984) examines the influence of adult age and experience, nest location, clutch size and laying sequence on breeding success. Information on migration between populations is not available however.

3.14 Little gull (*Larus minutes*)

Little gulls do not breed in the UK, but occur during migration, although large numbers can sometimes occur during the winter months. Baker *et al.* (2006) do not provide population estimates for this species. The European population is estimated to be within the region of 24,000 to 58,000 pairs (Burfield and van Bommel 2004). During certain weather conditions, very large numbers can occur in UK inshore and near offshore waters, such that 16% of the European population has been recorded flying past Flamborough Head in a single day for example (Maclean *et al.* 2006). They appear to winter offshore, but are not truly pelagic and it is after strong gales that they occur close to shore along much of the western seaboard of Europe from the North Sea south to the coast of West Africa and in the Mediterranean, Black and Caspian Seas (Lack 1986). Very large numbers pass along the French and Dutch coasts during late autumn, but their ultimate destination is unknown (Lack 1986).

There is very little information on demographic parameters associated with Little Gulls. Adult survivorship is estimated as 0.80 in Garthe and Hüppop (2004), but to our knowledge, no other data are available and no measures of variability in survival are provided either.

3.15 Black-headed gull (*Larus ridibundus*)

Baker *et al.* (2006) estimate the UK breeding population to comprise 138,014 pairs and the over-wintering population to be 1,697,797 individuals, the majority of which, at all times of year, but particularly during the breeding season, occur inland. During winter, they occupy a broad range of habitats, ranging from estuaries and coastal marshes, through grazing land and plough to inland wetlands, refuse tips and even parks and gardens (Lack 1986). Inland sites are often abandoned during harsh winter weather when freshwater sites are frozen. In such instances, larger numbers occur on the coast (Lack 1986). Ringing recoveries suggest that the majority of the UK breeding population over-winter in the UK, although there are some recoveries from France and Iberia (Lack 1986; Wernham *et al.* 2002). Winter numbers are bolstered by immigrants from northern Europe, Scandinavia, the Baltic states and Poland (Lack 1986; Wernham *et al.* 2002).

There is some information on survival, but not from UK populations. Adult survivorship is listed as 0.825 in Garthe and Hüppop (2004), which is derived from figures presented in Glutz von Blotzheim and Bauer (1982); the latter citation also provides information on variability. Prevot-Julliard *et al.* (1998) estimated adult survival in a population breeding in central France based on re-sightings of banded birds to be about 0.90 and attributes the higher than usual estimate to being a statistical by-product of differences in the probability of recapturing different age-classes. Beklova and Pikula (1980) examined the age-structure, mortality and survival of a population of black-headed gulls in the then Czechoslovakia. Clobert *et al.* (1994) use a statistical framework to estimate age-specific breeding probabilities from capture-recapture data, thus providing some information on instances of non-breeding. There is also some information on population turnover. Grosbois and Tavecchia (2003) use capture-recapture techniques to investigate the influence of local perturbations on site fidelity and settlement decisions of emigrants in a subdivided population. However, detailed information on migration between populations is lacking.

There is also some good information on breeding productivity, but again mostly from outside the British Isles. However, the number of pairs and the number of birds fledged per pair during 2004, 2005 and between 1986 and 2004 (means and standard errors) is given for 17 localities in the British Isles in Mavor *et al.* (2006). Thyen and Becker (2006) examined the effects of individual life-history traits on reproductive output and concluded that annual breeding success on the Wadden Sea coast is relatively constant at 0.7 fledglings per pair, but is positively related to clutch size, growth rate and rain during egg-laying and advanced chick-rearing phase. Indykiewicz (2005) examined factors determining the breeding success of an urban population of black-headed gulls in Poland and demonstrated that breeding success was 0.726 and each pair raised on average 1.81 offspring, although rates are highly variable. Muller *et al.* (2005) examines the influence of juvenile sex on nestling success in Germany and Prevot-Julliard *et al.* (2001) shows that hatching date influences the age of first reproduction in France. Lebreton (1996) derives results on age structure, net reproduction rate, generation time, and sensitivities using modelling techniques. Guthova (1993) examine variations in reproduction parameters of birds living in different conditions in the Czech and Slovak Republics. Lundberg and Vaisanen (1979) examine the influence of egg-size on chick mortality in Denmark and Lebreton and Isenmann (1976) examine the population dynamics of black-headed gulls in Camargue and these data are revisited by Lebreton (1996) to derive results on age structure, net reproduction rate, generation time, and sensitivities using modelling techniques.

3.16 Common gull (*Larus canus*)

Baker *et al.* (2006) estimate the UK breeding population to be 48,720 pairs and the over-wintering population to be 430,927 individuals, many of which occur inland. In summer, this species is predominantly confined to Scotland and Ireland, but during winter common gulls are abundant throughout the UK, often feeding far inland, but returning at dusk to roost on estuaries, lakes and reservoirs (Lack 1986). The majority of wintering birds come from breeding colonies in Scandinavia, Denmark and Germany, with smaller numbers from Holland, Russia and Iceland (Lack 1986; Wernham *et al.* 2002). The first migrants reach the UK in July and continue arriving until October, before departing in the first half of April (Lack 1986). The winter quarters of UK breeders is less clear, except in that ringing recoveries suggest that some Scottish breeders over-winter in Ireland (Lack 1986).

There is limited information on survival, but generally not from UK populations. Adult survivorship is listed as 0.80 in Garthe and Hüppop (2004), which is based on figures reported in Glutz von Blotzheim and Bauer's (1982) estimates of survival in Germany; the latter citation also provides information on variability. Kilpi and Saurola (1985) use ringing recoveries to determine movements and survival areas of Finnish common gulls.

There is fairly good information on breeding performance. The number of pairs and the number of birds fledged per pair during 2004, 2005 and between 1986 and 2004 (means and standard errors) is given for 12 localities in the British Isles in Mavor *et al.* (2006). Craik (2000a and b) provides information on breeding performance from several colonies throughout western Scotland. Rattiste (2004) examined the extent to which reproductive success varies with age and concluded that there is little relationship, with the only significant pattern being that ultimate breeders have low success. Kilpi (1995) examined the breeding success of colonial nesters in the northern Baltic and Rattiste and Lilleleht (1987) provide a brief account of the population ecology of common gulls in Estonia. Again there is no information from British populations. There is also no information on age-related survival and detailed information on the prevalence of non-breeders and migration between populations is also lacking.

3.17 Lesser black-backed gull (*Larus fuscus*)

Baker *et al.* (2006) estimate the UK breeding population to comprise 112,074 pairs and the over-wintering population to be 60,830 individuals, many of which occur inland. The seasonal status of lesser black-backed gulls in the UK has changed somewhat. It was formally a complete migrant with only small numbers of birds over-wintering in the UK, but now large numbers are seen in Britain in winter, mainly in the southwest (Lack 1986). In winter, lesser black-backed gulls are more common inland than on the coast, except in northwest England, where there is an obvious association with the large breeding colony on Walney Island in Cumbria (Lack 1986). The breeding distribution contrasts with the wintering distribution, with the majority occurring on the coast in W and NW England and southern Scotland (Lack 1986). Migrants of the British and three Scandinavian races reach Britain in October and continue passage for another three months, but numbers continue to fall until March (Lack 1986). Many UK breeders move south, over-wintering in France, Iberia and NW Africa (Wernham *et al.* 2002).

There is some information on survival. Adult survivorship is listed as 0.93 in Garthe and Hüppop (2004), which is derived from Wanless *et al.* (1996). Male and female survivorship is estimated as 90.7% (S.E. = 1.8) and 91.8 (S.E. = 1.6%) for females and males respectively (n = 104, Isle of May) in Wanless *et al.* (1996) giving a mean adult survival rate of 91.3% (S.E. = 1.2%) assuming no differences between sexes. Some information on pre-fledging survival is detailed in the studies concerned with reproductive success, described below, but information on immature survival is not available. There is information on incidences of non breeding in O'Connell *et al.* (1997) and Calladine and Harris (1997), but detailed information migration between populations is lacking.

There is good information on breeding productivity in relation to several factors. The number of pairs and the number of birds fledged per pair during 2004, 2005 and between 1986 and 2004 (means and standard errors) is given for 5 localities in the British Isles in Mavor *et al.* (2006). Wanless *et al.* (1996) showed that productivity varied greatly between years on the Isle of May, indicative of the varying control measures used. In relatively undisturbed areas, productivity varied from 0.54 to 1.04 young reared per nest. Kim and Monaghan (2006a) describe details of breeding performance of lesser black-backed gulls on one of the largest breeding colonies in the UK: Walney Island, Cumbria and Kim and Monaghan (2005) and (Calladine 1997) examine the effects of vegetation on breeding performance by the way in which it influences micro-climate on the same colony. Nager *et al.* (2000) examined the relationship between adult condition and brood sex-ratio on the survival of young and found that the pre-fledging survival of male chicks was strongly reduced in all-male broods reared by parents in poor condition. Pre-fledging survival of female chicks was, however, unaffected by parental condition or brood sex composition. Similarly, Bradbury and Griffiths (1999) show that sex-biased nestling mortality is influenced by hatching asynchrony and Griffiths (1992) shows how the overall sex ratio changed significantly from 0.484 (male/male + female) at hatching to 0.399 by fledging, probably due to male susceptibility to starvation. Bukacinski *et al.* (1998) showed that supplementary feeding enhances fledging success and Oro (1996) shows that breeding performance in the western Mediterranean is related to the availability of trawler discards. Hario (1994) examine how the breeding performance in the Gulf of Finland is influenced by Herring Gull predation. Bolton *et al.* (1993) examined how clutch size is influenced by body-condition and food supply and Bolton (1991) examines the relative importance of egg size and parental quality on chick survival. Hario (1990) in a ten-year study of breeding success in the Gulf of Finland revealed a high rate of parental failure in years of low rates of provisioning for the chicks. The parents ate their own eggs at the rate of 16% per annum (range 0-52%), and on average 13% of the chicks (range 0-25%) remained unfed. Houston *et al.* (1983) examined the effects of female body-condition on egg-laying, Bergman (1982) examines the population dynamics of lesser black-backed gulls in Finland and Brown (1967) examines breeding success in general.

3.18 Herring gull (*Larus argentatus*)

Baker *et al.* (2006) estimate the UK breeding population to comprise 139,309 pairs. In winter, numbers are bolstered by birds from northern Europe of race *argentatus* and the over-wintering population is estimated to be 378,748 individuals. Although numbers are highest on the coast, this species has a ubiquitous distribution, only absent from inland sites in highland areas. Most occur around urban areas (Lack 1986). Immediately after breeding, there are localised shifts in the breeding population towards favoured wintering locations, but thereafter little movement (Lack 1986). Ringing studies have revealed that a large proportion of the over-wintering population in Northern England, Scotland and London belong to the north European race *argentatus*, suggesting that winter influxes of birds from elsewhere account for the higher number of herring gulls present in the UK in winter (Lack 1986). Ringing recoveries suggest the majority of these come from Scandinavia (Wernham *et al.* 2002).

There is fairly good information on survival. Adult survivorship is listed as 0.93 in Garthe and Hüppop (2004), which is based on figures given in Glutz von Blotzheim and Bauer (1982). The latter citation also provides information on variability. Male and female survivorship is estimated as 89.8% (S.E. = 1.6) and 85.8 (S.E. = 2.0%) for females and males respectively on the Isle of May (Wanless *et al.* 1996) giving a mean adult survival rate of 88.0% (S.E.=1.3%) assuming no differences between sexes. Allard *et al.* (2006) established the adult survival of herring gulls breeding in the Canadian Arctic and Lebreton *et al*. (1995) performed a simultaneous survival rate analysis using dead recovery and live recapture data, although this involved a study of yellow-legged gulls *Larus cachinnans*, now considered by most authorities to be a separate species. Coulsen and Butterfield (1986) also examined adult survival. There is some information on pre-fledging survival, but none that we found on survival in post-fledged, but non-adult birds. Herbert and Barclay (1986) examined chick survival in relation to asynchronous and synchronous hatching, and Brouwer *et al.* (1995) examined chick survival in general. More details of pre-fledging survival are given in some of the studies examining breeding productivity described below. Calladine and Harris (1997) established that there are instances of intermittent breeding and Chabryz and Coulson (1976) determine aspects of survival and recruitment in herring gull populations, but there is no detailed information available on instances of non-breeding in herring gulls or on migration between populations.

There is good information on breeding performance. The number of pairs and the number of birds fledged per pair during 2004, 2005 and between 1986 and 2004 (means and standard errors) is given for 7 localities in the British Isles in Mavor *et al.* (2006). Several studies have examined the factors affecting breeding performance. These factors include both extrinsic factors such as food availability as well as intrinsic factors such as parental experience. Food-related studies include Regehr and Rodway (1999) who examined breeding performance during two years of delayed capelin *Mollatus villosus* arrival in the northwest Atlantic, Rodway and Regehr (1999) who examined the reproduction performance of food-stressed herring gulls, Kilpi and Ost (1998) who determined the effects of reduced availability of refuse on breeding output, Bukacinska *et al.* (1996) who examined attendance and diet in relation to breeding success, (Pons 1992) who determined the effects of changes in the availability of human refuse on breeding parameters and Vanklinken (1992) who examined the impact of additional food provisioning on breeding output on the Dutch Frisian Islands. Other extrinsic factors affecting reproductive success include nest site characteristics as demonstrated by Calladine (1997) who showed that this has an influence on breeding success. Graves *et al.* (1986) also suggested that nest site location affects reproductive success.

Studies relating to intrinsic factors such as parental experience include (Bogdanova *et al.* 2007) in which it is shown that the age of the incubating parents affects nestling survival, Bogdanova *et al.* (2006) in which it is established that parental age affects offspring performance through differences in egg quality, Kim and Monaghan (2005) who determined the interacting effects of nest shelter and breeder quality on behaviour and breeding performance, Risch and Rohwer (2000) who examined the effects of parental quality and egg size on growth and survival of chicks, Parsons (1975) examined the effects of asynchronous hatching on chick mortality, Parsons (1970) examined the effects of egg-size on post-hatching chick mortality and Davis (1975) who examined breeding success in relation to age and egg size. The sex of the first hatched brood also appears to have an important bearing on breeding productivity. For example, Kim and Monaghan (2006b) showed that when environmental conditions were relatively good, chick survival within broods was better when a female was first to hatch, an effect that was most obvious later in the season. When conditions were poorer however, sex of the first hatched chicks was not related to brood survival. Similarly, Royle and Hamer (1998) determined the effects of hatching asynchrony and sibling size hierarchies on reproductive success. Another intrinsic factor is egg size and geometry. Kilpi et al. (1996) examined the effects of egg size on reproductive success and Kilpi (1995) showed that egg symmetry predicts fledging success. Other studies include that by Wanless *et al.* (1996), which showed that productivity varied greatly between years on the Isle of May, indicative of the varying control measures used, Ellis and Good (2006) in which the breeding success of herring gulls on Appledore Island, Maine is established and Monaghan (1979) in which aspects of the breeding biology of herring gulls in urban colonies are examined. Several studies also suggest a degree of density-dependence in reproductive output**.** Wilkens and Exo (1998) examined the effects of population size and density dependence on breeding success on Mellum island in the German Wadden Sea, Kilpi (1989) examined the effects of varying pair numbers on reproduction, Coulson *et al.* (1982) examined changes in the breeding biology of herring gulls in relation to a reduction in colony size, Parsons (1976) examined breeding success in relation to nesting density and Brown (1967) determined the two-way relationship between breeding success and population growth.

More general studies on the population dynamics of herring gulls includes that by Kim and Monaghan (2006) who examined the breeding performance and demography in general of herring gulls breeding on Walney Island in Cumbria. Pons and Migot (1995) examined changes in survival and fecundity in a population subjected to various feeding conditions. Migot (1992) examined demographic changes in French herring gull populations, although these have no longer considered con-specific with UK herring gulls. Kilpi (1990) examined breeding biology in the Northern Baltic, Bergman (1982) examined population dynamics in Finland and Duncan (1978) determined the effects of culling herring gulls on recruitment and population dynamics.

3.19 Great black-backed gull (*Larus marinus*)

Baker *et al.* (2006) estimate the UK breeding population to comprise 17,160 pairs, which is derived from Mitchell *et al.* (2004), and the UK over-wintering population to consist of 43,156. Although as a breeder, it is almost exclusively coastal, during winter it is fairly widespread inland, although the major concentrations are still coastal, with sizeable numbers occurring on Shetland and Fair Isle (Lack 1986). During the breeding season, it is almost entirely absent from the east coast south of the Firth of Forth (Gibbons *et al.* 1993), but during winter it is fairly numerous in these areas, large numbers having been counted on the Northumberland and Durham coasts for example (Lack 1986). These are predominantly adult birds, and ringing recoveries suggest that they originate predominantly from the coast of Norway (Lack 1986; Wernham *et al.* 2002).

There is limited information on survival, but not from British populations. Adult survivorship is listed as 0.93 in Garthe and Hüppop (2004), which is based on figures given in Glutz von Blotzheim and Bauer's (1982). The latter citation also provides information on variability. Information on instances of non-breeding, on age-dependent survival and on migration between populations is lacking.

There is better information on reproductive performance, but again, mainly from non-British populations. However, the number of pairs and the number of birds fledged per pair during 2004, 2005 and between 1986 and 2004 (means and standard errors) is given for 13 localities in the British Isles in Mavor *et al.* (2006). Bergman (1982) examines the population dynamics of great black-backed gulls in Finland and Butler and Trivelpiece (1981) examined reproductive success in general. Ellis and Good (2006) examined the reproductive success of great black-backed gulls in Maine and Helberg *et al.* (2005) examined the relationship between reproductive performance and organochlorine contaminants in Germany. Finally, Regehr and Rodway (1999) examined breeding performance during two years of delayed capelin arrival in the northwest Atlantic.

3.20 Kittiwake (*Larus tridactyla*)

This species is almost exclusively coastal (Lack 1986). Baker *et al.* (2006) estimate the UK breeding population to comprise 366,832 pairs, which is derived from Mitchell *et al.* (2004), but no estimate of the over-wintering population is provided. Throughout the year, this species is almost exclusively coastal and it is also the most pelagic of British gulls, with wintering flocks occurring across the whole of the North Atlantic north of 40°N, often hundreds of kilometres from land. Extensive winter movements occur, with a long series of recoveries of birds ringed in the UK in Newfoundland, Labrador and Greenland (Lack 1986; Wernham *et al.* 2002). This oceanic distribution also involves kittiwakes from more northern colonies in Norway and arctic Russia and throughout the North Atlantic there is considerable mixing of birds from all breeding areas (Lack 1986). Prior to the 1960s, it was rare to see kittiwakes in UK coastal waters in November and December, except passing through a long distance offshore. However, more recently there has been a habitat switch, with small numbers now wintering around harbours and fish docks (Lack 1986).

There is good information on survival in relation to several factors. Adult survivorship is listed as 0.81 in Garthe and Hüppop (2004), which is based on figures given in del Hoyo *et al.* (1996). The latter citation also provides information on variability. Frederiksen *et al.* (2004) gives information on survival in relation to changes in industrial fisheries. Harris *et al.* (2000) provides estimates of adult survival between 1986 and 1996 from the Isle of May. Sandvik *et al.* (2005) assessed the effects of climate on adult survival and Oro and Furness (2002) examined the influences of food availability and predation on survival. Coulson (2002) examined why adults survive so long but breed so poorly in the Pacific and Coulson (2001) examined whether density-dependent mortality occurs in breeding kittiwakes. Coulson and Strowger (1999) examined the annual mortality rate of Kittiwakes in NE England from 1954 to 1998 and Golet *et al.* (1998) examined the survival costs of chick rearing. Hatch *et al.* (1993) determined adult survival in a Pacific colony and Danchin and Monnat 1992) used capture-mark-recapture models and Leslie matrix models to estimate annual adult survival rates and the demographic balance in a flourishing and in a nearby declining colony. Coulson and Wooller 1976) determined differential survival rates with age.

There is also fairly good information on instances on non-breeding on patterns of recruitment. McCoy *et al.* (2005) determines general dispersal patterns and Cam *et al.* (2002), the influence of behaviour on recruitment and production. Boulinier *et al.* (2002) tested the effect of conspecific reproductive success on dispersal and recruitment decisions, Porter (1990) examined patterns of recruitment and Porter and Coulson (1987) determined long-term changes in recruitment to a breeding group. Cam *et al.* (1998) examined reasons for non-breeding, but then later point out that unless survival before full recruitment is known to be identical in the groups, inferences about the causes of variation in realized age of first breeding among groups are difficult (Cam *et al.* 2005).

There is also good information on breeding performance. The number of pairs and the number of birds fledged per pair during 2004, 2005 and between 1986 and 2004 (means and standard errors) is given for 41 localities in the British Isles in Mavor *et al.* (2006). Breeding performance has also been examined in relation to various factors that might affect it, notably food availability For example, Hamer *et al.* (1993) examined the influence of food availability on breeding ecology in general and Gill *et al.* (2002) examined the sensitivity of breeding parameters to food supply. Similarly, Frederiksen *et al.* (2005b) assessed regional patterns of breeding success in relation to variability in sandeel recruitment and Poloczanska *et al.* (2004) used stochastic models to evaluate the likely effect of varying fishing mortality and breeding success. Gill and Hatch (2002) examined the influence of supplementary feeding on breeding performance and Lewis *et al.* (2001) examined diet in relation to breeding performance in the North Sea. Hipfner *et al.* (2000) examined breeding success at a colony in Labrador during a period of low capelin availability and Rindorf *et al.* (2000) examined the effects of changes in sandeel availability on reproductive output. Similarly, Massaro *et al.* (2000) determined that delayed capelin availability influences predatory behaviour of large gulls on black-legged kittiwakes causing a reduction in kittiwake breeding success and Suryan *et al.* (2000) examined the effects of prey-switching and foraging strategies on reproductive success. Regehr and Montevecchi (1997) examined the interactive effects of food shortage and predation on breeding failure, Harris and Wanless (1997) examined breeding success, diet, and brood over an 11-year period and Danchin (1992) examined whether food shortage was a factor in the 1988 breeding failure in Shetland. Thompson and Walsh (2000) provide information on breeding success between 1978 and 1998 on Orkney.

Another factor which has been the subject of considerable study in relation to kittiwake breeding performance is that of parental experience. For example, Coulson (1966) determined the influence of pair-bond and age on breeding biology and Coulson and Porter (1985) examined reproductive success in relation to clutch size, chick-growth rates and parental quality. Thomas (1983) examined the relationship between breeding experience, egg volume and reproductive success and Wooller and Coulson (1977) determined factors affecting the age of first breeding. Naves *et al.* (2007) assessed whether breeding experience, mate change, individual adult quality and prior residence affects breeding success and Naves *et al.* (2006) assessed whether breeding failure is associated with divorce and dispersal.

There are also several general studies on breeding success. Coulson and Thomas (1985) performed a long-term (31 year study) investigating breeding biology and Barrett and Runde (1980) examined the growth and survival of nestlings in Norway. Harris and Wanless (1990) determined changes in the breeding success of British kittiwakes between 1986 and 1988 and Murphy *et al.* (1991) demonstrated that there was high inter-annual variability in reproductive success at a colony in Alaska. Suryan *et al.* (2006) assessed the relative roles of bottom-up and top-down factors in determining reproductive success and Coulson and Fairweather (2001) determined that reduced reproductive performance occurs prior to death. Danchin *et al.* (1998) examined the effects of habitat selection on reproductive success and Neuman *et al.* (1998) examined reproductive success in Newfoundland.

There are also several studies examining the population dynamics of kittiwakes in general. Frederiksen *et al.* (2005a) demonstrated that there can be considerable inter-population differences in demographic parameters and Frederiksen *et al.* (2004) use demographic data collected between 1986 and 2002 to determine the extent to which industrial fisheries have caused kittiwakes to decline. Wintrebert *et al.* (2005) jointly model breeding and survival and Suryan and Irons (2001) examined the population dynamics of 25 colonies in the Prince William Sound, Alaska.

3.21 Sandwich tern (*Sterna sandvicensis*)

This species is predominantly a breeding visitor to the UK, but numbers are somewhat bolstered by passage birds. The vast majority occur in coastal areas. Baker *et al.* (2006) estimate the UK breeding population to comprise 12,490 pairs, which is derived from Mitchell *et al.* (2004), but no estimates for other times of year are provided. Sandwich Terns are migratory throughout the western Palaearctic, with birds from Britain, Ireland, the Netherlands, Denmark and Germany all having common over-wintering grounds in West Africa (Wernham *et al.* 2002). Juveniles of Sandwich Terns breeding in the UK begin post-fledging dispersal in late June across the North Sea to Denmark and the Netherlands, with some birds from the Netherlands also arriving in the UK. Thereafter, they are joined by adult birds prior to migrating to their wintering quarters. Sandwich terns ringed in Britain have been recovered in subsequent breeding seasons in Denmark, the Netherlands, Belgium and France and birds ringed abroad, but recovered in Britain have come from Belgium, Denmark, Germany and the Netherlands (Wernham *et al.* 2002). This would suggest that there is at least some inter-change between breeding colonies throughout NW Europe.

The only information we found on survival was that listed for adult survivorship in Garthe and Hüppop (2004) as 0.88. No information on variability is provided. However, there is some information on breeding performance. The number of pairs and the number of birds fledged per pair during 2004, 2005 and between 1986 and 2004 (means and standard errors) is given for 13 localities in the British Isles in Mavor *et al.* (2006). Stienen and Brenninkmeijer (2006) examined the effect of brood size and hatching sequence on pre-fledging mortality and Stienen and Brenninkmeijer (2002) examined variations in growth and the consequences for pre- and post-fledging mortality in the Dutch Wadden Sea Gauzer (1989) determined that asynchronous hatching affects juvenile mortality. Estimates of breeding success from colonies throughout Britain between 1990 and 1998 have been made as part of the Seabird Monitoring Programme (Ratcliffe *et al.* 2000). Detailed information on migration between populations and on instances of non-breeding is lacking however.

3.22 Arctic tern (*Sterna paradisaea*)

This species is a breeding visitor to the UK, with the vast majority occurring in coastal areas. Baker *et al.* (2006) estimate the UK breeding population to consist of 53,338 pairs, which is derived from Mitchell *et al.* (2004). Artic terns undergo one of the most extensive migratory journeys of any bird species, with the majority of UK breeders moving south to Antarctic waters during the boreal winter. The UK lies at the southern extremities of this species’ breeding range as it essentially has a circumpolar breeding range, breeding further north than any other species (Wernham *et al.* 2002). Birds from the Bering Sea and eastern Siberia move south along the American Pacific coast, whereas many birds from the Nearctic join those from northern Europe and western Siberia and migrate south along the coasts of western Europe. Although most ringing recoveries of birds in the UK were ringed as pulli in the UK, it seems likely that the migratory population is bolstered by birds from elsewhere, but, as with the UK population the majority of these migrate far offshore (Wernham *et al.* 2002). Birds return to their breeding grounds in March, essentially retracing their autumn migratory route, although it has been suggested that a few migrate northwards through the Indian Ocean and then pass overland at high altitudes, accounting for sporadic recoveries from the Urals (Wernham *et al.* 2002). At most times of year the bird is essentially coastal or pelagic, but large numbers recorded at inland reservoirs in central England, suggest that this species does migrate overland and that such observations are indicative of poor flying conditions at sea or at high altitude (Wernham *et al.* 2002).

There is some information on survival. Adult survivorship is listed as 0.875 in Garthe and Hüppop (2004), which is based on figures given in del Hoyo *et al* (2006). The latter citation also provides information on variability. Coulson and Horobin (1976) examined the influence of age on reproduction and survival. There is also some additional information on breeding productivity. The number of pairs and the number of birds fledged per pair during 2004, 2005 and between 1986 and 2004 (means and standard errors) is given for 15 localities in the British Isles in Mavor *et al.* (2006). Nordstrom *et al.* (2004) examined the influence of removing American Mink *Mustela vison* on breeding success in Finland and Suddaby and Ratcliffe (1997) examined the effects of fluctuating food availability on breeding. Robinson *et al.* (2001) examined the effects of food provisioning rates and parental brooding on brood size and Robinson and Hamer (2000) of this on chick growth. Bunin and Boates (1994) examined effects of nesting location on breeding success and Monaghan *et al.* (1989) examined the relationship between food-supply, reproductive effort and breeding success. Information on instances of non-breeding and on migration between populations is lacking.

3.23 Little tern (*Sterna albifrons*)

This species is a breeding visitor to the UK, with the vast majority occurring in coastal areas. Baker *et al.* (2006) estimate the UK breeding population to consist of 1,947 pairs, which is derived from Mitchell *et al.* (2004). Little terns are rarely recorded far out to sea, and the general pattern of movement is typical of a bird migrating to spend the winter in near-shore areas of western Africa, showing a dispersal phase when immature: most ringing recoveries are from France, Portugal and NW Africa, generally progressively later in the season as the birds move southwards (Wernham *et al.* 2002). Large flocks of little terns have been recorded in the Netherlands in August, suggesting that it may be a staging-post for birds from a wider area, but no such concentrations have been recorded in the UK, and it is generally thought that most birds occurring in the UK during migration breed locally (Wernham *et al.* 2002).

There is no information on survivorship, but some information on reproductive performance. The number of pairs and the number of birds fledged per pair during 2004, 2005 and between 1986 and 2004 (means and standard errors) is given for 20 localities in the British Isles in Mavor *et al.* (2006). Medeiros *et al.* (2007) examined the impact of human disturbance on nesting success in Portugal and Oro *et al.* (2004) colony site selection, clutch size and egg size in the Ebro Delta. Hong *et al.* (1998) examined the effects of clutch size and egg-laying order on the breeding success in Korea and Holloway (1993) examined variable breeding success in south-east India. Estimates of breeding success from colonies throughout Britain between 1990 and as part of the Seabird Monitoring Programme (Ratcliffe *et al.* 2000) have shown overall annual breeding success to fluctuate between 0.11 and 0.70 chicks fledged per pair. Information on migration between populations and on instances of non-breeding is lacking, although some information on more local movements is given in Perrow *et al.* (2006).

3.24 Guillemot (*Uria aalge*)

Guillemots are resident and exclusively coastal and marine species in the UK. Baker *et al.* (2006) estimate the UK breeding population to comprise 1,420,900 individuals, which is derived from Mitchell *et al.* (2004), but no estimates of the number of birds in winter are provided. During the breeding season, numbers are generally concentrated around breeding colonies (Gibbons *et al.* 1993), but during winter this species is far more widespread with significant numbers occurring in SE England even though non breed between Flamborough Head and the Isle of Wight (Lack 1986). Guillemots leave their colonies between June and August, forming flightless moulting flocks. They then return to their breeding colonies from October on the East coast, but November-December on the west coast and immediately begin to moult back into breeding plumage. These birds generally comprise of breeding adults returning to their nest sites (Harris and Wanless 1984) and these late autumn returns have become earlier in recent decades (Lack 1986). They then disperse more widely during winter, with first year birds dispersing the furthest (Lack 1986; Wernham *et al.* 2002). However, ringing recoveries suggest that the majority of the UK breeding population over-winter in Britain, although the winter population in the North Sea is also augmented by birds from the Faeroes, Norway and Heligoland (Lack 1986; Wernham *et al.* 2002).

There is good information on survival from several populations. Adult survivorship is listed as 0.885 in Garthe and Hüppop (2004), which is based on figures given in del Hoyo *et al.* (1996). The latter citation also provides information on variability. Harris *et al.* (2000) provides estimates of adult survival between 1986 and 1996 from the Isle of May. Robertson *et al.* (2006) examined local survival rates in Newfoundland and Sandvik *et al.* (2005) determined the impact of climate change on adult survival in the North Atlantic. Osterblom *et al.* (2004) examined adult survival in relation to avian cholera in the Baltic and Harris *et al.* (2000) examined the survival of adults at three Scottish colonies. Sydeman (1993) determined survivorship in California and Harris *et al.* (1992) determined post-fledging survival in relation to hatching date and growth in Scotland. Harris and Bailey (1992) determined mortality rates in relation to fish abundance in the North Sea and Piatt and van Pelt (1997) describes an instance of mass-mortality in Alaska, thus illustrating variability in survivorship with feeding conditions. There is also information on age-dependent survival and non-breeding. Harris and Wanless (1995) assessed survival and non-breeding on the Isle of May, Harris *et al.* (1994) determined the age of first breeding and Crespin *et al.* (2006b) link adult mortality with age in this same population.

There is also good information on breeding productivity in relation to both intrinsic and extrinsic factors. The number of pairs and the number of birds fledged per pair during 2004, 2005 and between 1986 and 2004 (means and standard errors) is given for 11 localities in the British Isles in Mavor *et al.* (2006). Crespin *et al.* (2006b) determined that there is reduced breeding success with age in a population on the Isle of May and Rindorf *et al.* (2000) the effects of changes in sandeel availability on reproductive output. Regehr and Rodway (1999) examined breeding performance in relation to delayed capelin arrival. Harris *et al.* (1997b) determine the effects of nest-site characteristics and duration of use on breeding success. Parrish (1995) examined the influence of group size and habitat type on reproductive success and Murphy and Schauer (1994) examined breeding success in Alaska between 1975-1991. Uttley *et al.* (1994) examined the effects of food abundance on breeding performance and Wanless and Harris (1988) determine the importance of laying-date on breeding success. Hedgren (1981) examined the effects of fledging weight and time of fledging on survival of chicks, Birkhead (1977) determined the effects of habitat and density on breeding success and Crespin *et al.* (2006b) link adult mortality and reduced breeding success with age in a population on the Isle of May. Thompson and Walsh (2000) provide information on breeding success between 1978 and 1998 on Orkney. Hipfner and Bryant (1999) provide general information on the breeding biology of guillemots at a colony in the Northwest Atlantic.

There is also some information on migration between populations. Crespin *et al.* (2006a) demonstrated how recruitment to a population depends upon environmental factors and population size, Halley *et al.* 1995) examined colony attendance patterns and recruitment in immature birds and Halley and Harris (1993) determined inter-colony movements, again of immature birds. There are also several studies dealing with the population dynamics of guillemots in general. Harris and Wanless (1988) discuss the breeding biology of guillemots on the Isle of May over a six-year period, Hatchwell and Birkhead (1991) determined the population-dynamics of guillemots on Skomer Island in Wales and Birkhead and Hudson (1977) detail general population parameters.

3.25 Razorbill (*Alca torda*)

Razorbills are a resident and exclusively coastal and marine species in the UK. Baker *et al.* (2006) estimate the UK breeding population to comprise 188,576 individuals, which is derived from Mitchell *et al.* (2004), but no estimates of the number of birds in winter are provided. The distribution of razorbills in the UK is approximately similar to that of guillemots, both in winter and summer, and as such, this species is generally more widespread during winter than in summer

(Lack 1986). This species is particularly prone to wrecks during unfavourable weather conditions, when large numbers are recorded close to land (Lack 1986). Like guillemots, razorbills leave their colonies in late August to moult and then become flightless, but unlike the former species, they shun land until February or March, although at a few colonies in E Scotland, they also return to their breeding ledges in October or November, but more sporadically (Lack 1986). Migration patterns are complicated, but generally first year birds move further than adults, with young from the Irish Sea colonies over-wintering off France, Iberia and in the Mediterranean, whereas adults rarely move further than France (Wernham *et al.* 2002). Many northern British razorbills, visit Norway, but some are recovered further south, and also one recovery from Greenland (Wernham *et al.* 2002). Ringing recoveries also suggest that some Russian, Norwegian and probably many Icelandic Razorbills winter around Britain (Lack 1986; Wernham 2002).

There is some information on survival. Adult survivorship is listed as 0.905 in Garthe and Hüppop (2004), which is based on figures given in del Hoyo *et al.* (1996). The latter citation also provides information on variability. Harris *et al.* (2000) provides estimates of adult survival between 1986 and 1996 from the Isle of May. Sandvik *et al.* (2005) determined the impact of climate change on survival in the North Atlantic and Chapdelaine (1997) used ringing recoveries to estimate the survival of adult and immatures in the western Atlantic. Lloyd and Hipfner and Bryant (1999) provide general information on the breeding biology of razorbills at a colony in the Northwest Atlantic. A brief overview of literature giving details of adult survivorship is given in Mitchell *et al.* (2004). Perrins (1977) uses ringing recoveries to determine the survival and age of first-breeding, but detailed information on incidences of non-breeding and immigration to / emigration from UK populations is lacking.

There is also some information on breeding productivity. The number of pairs and the number of birds fledged per pair during 2004, 2005 and between 1986 and 2004 (means and standard errors) is given for seven localities in the British Isles in Mavor *et al.* (2006). Harris and Wanless (1989) detail the breeding biology of razorbills on the Isle of May and Hudson (1982) determines the influence of nest-site characteristics on breeding success. Thompson and Walsh (2000) provide information on breeding success between 1978 and 1998 on Orkney.

3.26 Puffin (*Fratercula arctica*)

Puffins are resident and exclusively coastal and marine species in the UK. Baker *et al.* (2006) estimate the UK breeding population to comprise 580,799 pairs, which is derived from Mitchell *et al.* (2004), but no estimates of the number of birds in winter are provided. During the breeding season, most occur around breeding colonies (Gibbons *et al.* 1993). During winter, puffins are generally pelagic, with those recorded close to land generally being sick or oil-slicked individuals or birds blown off course during unfavourable weather conditions, although as with Razorbills, large wrecks can occur (Lack 1986). Puffins depart British colonies in August and do not return until spring, with the main moult, which renders the bird flightless, occurring during the breeding season. Puffins nesting in the west of Britain and in Ireland disperse very widely in winter, with ringing recoveries from Newfoundland to Italy and from Greenland to the Canary Islands. East coast birds remain mostly in the North Sea where they are joined by some Norwegian birds, but increasingly numbers pass through the English Channel on route to the Bay of Biscay. None appear to over-winter in the Irish Sea (Lack 1986; Wernham *et al.* 2002).

There is fairly good information on survival in relation to several factors. Adult survivorship is listed as 0.95 in Garthe and Hüppop (2004), which is based on figures given in del Hoyo *et al.* (1996). The latter citation also provides information on variability. Harris *et al.* (2000) provides estimates of adult survival between 1986 and 1996 from the Isle of May. Harris *et al.* (2005) examined the effects of wintering area and climate on survival and similarly, Sandvik *et al.* (2005) examined the impact of climate on survival in the North Atlantic. Breton *et al.* (2005) provide adult survival estimates from two colonies in Maine. There is also some survival information relating specifically to UK populations. Harris *et al.* (1997a) examined factors influencing the survival of puffins on the Isle of May over a 20-year period and Harris and Bailey (1992) examined mortality rates in relation to food availability in the North Sea. There is also information on age-related survival. Harris and Rothery (1985) examined post-fledging survival in relation to hatching-date and growth and Harris (1983) determined the biology and survival of immature birds. There is some information on migration between populations: Breton *et al.* (2006) models survival and movement of a meta-population. However detailed information from UK populations specifically is lacking.

There is also relatively good information on breeding productivity in relation to several factors. The number of pairs and the number of birds fledged per pair during 2004, 2005 and between 1986 and 2004 (means and standard errors) is given for 7 localities in the British Isles in Mavor *et al.* (2006). Baillie and Jones (2003; 2004) and Regehr and Rodway (1999) examined the effects of capelin abundance on reproductive success. Finney *et al.* (2001) examined the impact of gulls on reproductive performance. Rodway *et al.* (1998) examined intra-colony variations in breeding performance and Harris *et al.* (1998) examined long-term variations in the breeding-performance of puffins on St Kilda. Barrett *et al.* (1987) and Barrett (2001) examined the breeding demography of Norwegian puffins and Harris (1980) determined the breeding performance of puffins in relation to nest density, laying date and year. Lastly, Nettlesh (1972) determined the breeding success of puffins in different habitats in Newfoundland.

3.26 Summary of data availability

A summary of data availability is given in Table 2. For all species with the exception of little tern, there is good information on adult survival, although for little gull there is only limited information. There is less information for age-related survival, with no information for red-throated diver, black-throated diver, great crested grebe, eider, arctic skua, little gull, common gull, lesser black-backed gull, herring gull, great black-backed gull, sandwich tern and little tern and only limited information for gannet, common scoter and velvet scoter. For all species with the exception of great crested grebe and little gull there is good information on productivity, but there is less information on the proportion of the total population that actually breed, with such data only available comprehensively for cormorant, eider, arctic skua, great skua, lesser black-backed gull, kittiwake and guillemot and in a limited way for herring gull, razorbill and puffin. There is even less information on migration between populations. Only for cormorant, kittiwake and guillemot could such data be considered reasonable and additionally only for fulmar, shag, eider, black-headed gull, herring gull and puffin is any such data available at all. There is also only limited data on density-dependent changes in population-parameters. In relation to survival, only for cormorant, shag and kittiwake is such data comprehensive and in relation to productivity only for eider, herring gull, kittiwake, guillemot and puffin.

Table 2. Demographic data availability (mean and variance) for species likely to be vulnerable to offshore windfarms. A score had been calculated for each species to indicate the overall quality of data available. The score is the product of a data availability score (Yes=2, Some=1, No=0) and a score which indicates the likely importance of each of the demographic components for carrying out population viability analysis, judged through expert opinion (5=very important to 0=no importance). Thus a high score indicates good data availability. The maximum score that can be attained is 46.

	Adult survival	Productivity	Age-dependent survival	Age-dependent productivity	Incidences of non-breeding	Migration between meta-populations	Density-dependent survival	Density-dependent productivity	Score
Red-throated diver	Y	Y	N	N	N	N	N	N	16
Black-throated diver	Y	Y	N	S	N	N	N	N	16
Great Crested Grebe	Y	N	N	N	N	N	N	N	6
Fulmar	Y	Y	Y	Y	N	S	N	N	26
Gannet	Y	Y	S	N	N	N	N	N	18
Cormorant	Y	Y	Y	Y	Y	Y	Y	N	42
Shag	Y	Y	Y	Y	N	Y	Y	N	34
Eider	Y	Y	N	S	Y	S	N	Y	30
Common scoter	Y	Y	S	N	N	N	N	N	18
Velvet scoter	Y	Y	S	N	N	N	N	N	17
Arctic skua	Y	Y	N	Y	Y	N	N	N	28
Great skua	Y	Y	Y	Y	Y	N	S	N	35
Little gull	S	N	N	N	N	N	N	N	4
Black-headed gull	Y	Y	Y	Y	N	S	N	N	26
Common gull	Y	Y	N	Y	N	N	N	N	20
Lesser black-backed gull	Y	Y	N	Y	Y	N	N	N	24
Herring gull	Y	Y	N	Y	S	S	N	Y	26
Great black-backed gull	Y	Y	N	N	N	N	N	N	14
Kittiwake	Y	Y	Y	Y	Y	Y	Y	Y	46
Sandwich tern	Y	Y	N	N	N	N	N	N	14
Arctic tern	Y	Y	Y	N	N	N	N	N	20
Little tern	N	Y	N	N	N	N	N	N	8
Guillemot	Y	Y	Y	Y	Y	Y	N	Y	40
Razorbill	Y	Y	Y	B	S	N	N	N	26
Puffin	Y	Y	Y	N	S	S	S	Y	37

Y = Good information available, S = Some information, N = No information
🟧 = Excellent score, ☐ = Good score, ☐ = Reasonable score, ☐ = Poor Score

4. Conclusions

In general there is information on much of the demographic data needed to inform a basic population viability analysis, and overall a population viability approach to determining the impact of offshore windfarms on seabird populations should be possible. In so doing, it would be advisable to use the software package ULM, as this package allows the most sophisticated means of incorporating age- and density-dependent differences in demographic factors.

Although sufficient data exist to ensure that a PVA approach could be used to assess the extent to which windfarms impact populations directly, through for example the mortality of a certain number of individuals, indirect impacts will be harder to assess. To illustrate this point, consider a scenario where collision with wind turbines results in the demise of 10% of individuals of a population per year. Using PVAs, the extent to which this is compensated for by births in the population could be assessed. However, it is also possible that the death of a certain number of individuals will result in reduced competition for resources amongst the remaining individuals in the population, thus increasing annual survival rates and / or productivity in a density-dependent manner. Conversely, it is also possible that collisions could reduce productivity if mortality occurs during the breeding season as it could result in the starvation of pre-fledged young. Similar problems arise if one were to consider the extent to which windfarm induced displacement alters demographic parameters. Displacement itself is not a direct cause of mortality, but mortality may result because increased competition for resources in areas the birds are displaced to, which may be less favourable or host potentially competing individuals already. At present, although good data on many demographic parameters exist, the extent to which collisions cause mortality indirectly can only be inferred indirectly through proxy methods, by making assumptions about the extent to which a population and surrounding populations are at carrying-capacity for example. Determining the impact of displacement, also necessitates assumptions to be made regarding the extent to which birds are likely to disperse to neighbouring areas, as at present no such data are available.

Another critical issue in determining the impact of windfarms on bird populations, is the question of migration between populations, and what exactly constitutes a population as opposed to say one colony, which forms part of a larger population. Answering this question to a large extent, involves considering two issues. Firstly, what population are we interested in? Are we trying to determine the impact on the British population as a whole or are we trying to determine regional impacts on one meta-population? Secondly, one needs to understand movements between each of the populations or meta-populations. To determine the overall impact on one population, the extent to which interchange with neighbouring populations must be determined, as a potential reduction in one localised population could be compensated for if sufficient migration from other populations occurs. Although for some species such as kittiwake, there is good information available on inter-colony movements, inter-population migration rates themselves are likely to be density-dependent in so much as a reduction in the number of individuals at one colony is likely to attract individuals, from neighbouring colonies, particularly young birds that have not established site-fidelity because of the benefits in terms of reduced competition for resources. Such data are lacking at present.

Although there are difficulties associated with determining the indirect effects of offshore windfarms on bird populations, PVAs nevertheless provide a very useful framework in which such issues can be explored. Even if precise parameter values are not known, reasonable estimates can be incorporated into PVA models, and the sensitivity of results to variations in these values assessed. This has the dual advantage of enabling the range of likely impacts on bird populations to be determined in terms of worst-case or best-case scenarios, but also allows an assessment of what the greatest uncertainties are in terms of determining the impact of windfarms on bird populations, thus enabling future offshore wind-farm related research to be more focused. In-so-doing however, we caution against a “black-box” approach. Values should not be entered into PVA models and answers widely applied without critical assessment.

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