The Feasibility of Integrated Population Monitoring of Britain's Seabirds

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1. SUMMARY

1. Britain and Ireland have some of the largest seabird colonies in Europe and are home to majority of the world population of three species (Manx Shearwater, Gannet and Great Skua) and numbers of many more are important in a European context. Seabird populations in Britain face a large number of threats, including changing resource distribution in response to increasing sea temperatures, pollution and nest predation, particularly from introduced predators. In order to identify the threats that are important in driving a population change it is necessary to understand the demographic processes (i.e. survival and productivity) underlying them.

2. There is no overall framework for demographic monitoring of seabird populations in Britain (unlike for many terrestrial species). However, a census of (almost) all colonies has been organised at roughly fifteen year intervals since the late 1960s and breeding numbers and productivity are monitored at a sample of colonies under the Seabird Monitoring Programme (SMP). Data on survival rates has been collected at a relatively limited number of sites, including the four 'key' sites within the SMP. Data from these sites have had a large impact on our understanding of seabird population processes and show the benefit of long-term collection of demographic data.

3. In many seabird populations, changes in abundance and productivity (and probably survival) vary between regions, so a network of sites will be required to fully understand changes in seabird status. Because of their life histories, productivity in seabirds is often quite variable but variation in survival has the greatest impacts on population size. Annual survival usually varies increases from fledging up to breeding age, but may decrease in older individuals. Estimating age-related annual survival of immature birds is challenging because reporting rates also often vary between age-classes, but in at least some cases, only the aggregate survival of birds until breeding age (a measure of recruitment) may be necessary as this is often the key demographic parameter that needs to be estimated.

4. There are three main aims in calculating survival rates: to understand historical changes in relation to changes in environmental conditions; to monitor future changes in survival rates (usually on an annual basis); and to provide parameters for population models. Survival rates may be estimated either from re-sightings (or re-captures) of marked birds or from recoveries of dead metal-ringed birds. The former are often able to generate more detailed information (e.g. on age-specific rates), but suffer from generally under-estimating 'true' survival rates (though the extent of this varies between species), for which the latter are less biased. Increasingly, both mark-recapture and mark-recovery data are being used jointly to estimate survival rates and this has considerable promise for estimating seabird survival rates.

5. Data gathered through the national ringing scheme and individual colour-mark studies have previously been used to calculate historical changes in survival rates, most successfully on the Isle of May (an SMP key monitoring site). However, while some analyses have been undertaken, more can be made of this archive. In particular, analyses of changes in survival (and other demographic parameters) for Manx Shearwater, Herring and Lesser Black-backed Gulls, and Cormorant would be useful, as these are species of conservation/management interest and sample sizes are sufficient to support survival modelling. There appears to be no published information on survival for a few species, including greater black-backed gull and red-throated diver, so although there are limited ring-recovery data, any information on survival rates they yield will be useful[1].

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[1] Analyses of Manx Shearwater and Red-throated Diver survival rates have recently been commenced.

6. Future annual monitoring of survival rates is likely to be possible for a small suite of species, including: Fulmar, Manx Shearwater, Shag, Kittiwake, Arctic Skua and Guillemot by combining mark-recapture studies with more general mark-recovery information. This would involve expanding the network of key monitoring sites to make it geographically more representative. This would probably need to involve volunteer ringers and would require an element of training and capacity building. The Re-trapping Adults for Survival (RAS) programme would form a useful model for this, and indeed already includes a small number of seabird projects. Ringing of a greater number of adults of all species is to be encouraged as this enables age-specific survival rates to be estimated with much greater precision.

7. Population modelling has tended to involve separate analyses of abundance, survival and productivity. However, recently, methodological advances (particularly in Bayesian statistics) allow these parameters to be analysed simultaneously, resulting in much greater analytical and modelling power. Although the development of Integrated Population Models (IPMs) for seabirds is likely to take much research effort, there is great scope for furthering our understanding of seabird populations, largely using existing data. Work on an IPM for Guillemot is underway, and priorities for future modelling could include Cormorant, Kittiwake (building on the extensive work already conducted) and Herring and Lesser Black-backed Gulls.

2.   INTRODUCTION

Britain's long, diverse, and often remote, coastline offer a variety of nesting opportunities for a wide range of seabird species. The marine environment, surrounding its coast includes a complex array of hydrographical features, such as thermal and saline fronts and deep water and surface currents, which vary seasonally and spatially provide rich concentrations of plankton and fish as a feeding resource. Around 8 million seabirds of 25 or so species breed around the shores of Britain and three: Manx Shearwater, Gannet and Great Skua[2], have more than half of their global population in Britain and Ireland (Mitchell *et al.* 2004). Within Europe, colonies in Britain and Ireland hold around half the total number of breeding pairs, so clearly seabirds are an important part of our fauna.

The United Kingdom has a number of international obligations, such as EC Directive 79/409 ('The Birds Directive'), to monitor its populations of seabirds and to take measures to maintain or improve their conservation status. There is a long tradition of monitoring seabirds in Britain, with counts of some colonies having been maintained for several decades (e.g. Perrins *et al..* 1991). Indeed, three more or less complete censuses of the entire British and Irish seabird assemblage have been undertaken at roughly fifteen year intervals (Cramp *et al.* 1974; Lloyd *et al.* 1991; Mitchell *et al.* 2004). Such population monitoring is clearly necessary for documenting population trends, but for a number of reasons, demographic monitoring provides a necessary complement to counts of, mostly breeding, birds.

Changes in population numbers of all bird species are determined by a combination of survival (animals leaving the population) and productivity (animals entering the population). For populations at a local and regional scale, immigration and emigration of individuals from elsewhere may also play a part in determining numbers in that area (notably in a UK context, Cormorant). To understand the reasons behind population change, and to formulate effective management plans in response to such changes, it is necessary to understand the demographic mechanisms causing those changes.

2.1   Demographic and Population Monitoring

Most information for demographic models employed in population management comes from pre-existing long-term monitoring programmes for two reasons. Firstly, an historic component is often required to provide a contrast to conditions currently experienced and, secondly, collecting demographic data *de novo* for a particular project is usually expensive and time-consuming, with a lag of several years sometimes being necessary before sufficient data is obtained.

Demographic monitoring is a major component of Integrated Population Monitoring (IPM, Baillie 2001). At one level, this simply provides a framework within which to collect demographic data in a structured way. At another it allows a complete picture of a species life-cycle to be constructed, and the relative importance of environmental influences on each stage to be assessed. Previously this has been accomplished by examining data on each parameter in turn, but recent advances in statistical techniques are beginning to allow the various types of demographic data to be brought together within a single statistical framework greatly increasingly their power to identify drivers of demographic change (e.g. Brooks *et al.* 2004; Reynolds *et al.* in press). Such integrated analyses make best use of the data by recognising, for example, that productivity data give some information about population state (populations are generally higher following a year of good productivity).

A good example of the utility of demographic monitoring in understanding seabird population change is provided by Frederiksen *et al.* (2004a), who sought to understand why numbers of Kittiwakes in colonies bordering the North Sea had declined by more than 50% over a 15 year period. Both environmental (increasing sea temperatures causing shifts in the sandeel biomass) and anthropogenic (sandeel fisheries) factors were examined. By studying the demographic data that had been collected,

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[2] Where scientific names are not given in the text, these can be found, along with 'full' English names in Table 1.

Frederiksen showed that the fisheries were not (directly) responsible for the change in population numbers, but that changing fisheries management may be necessary in order to improve the conservation status of the Kittiwake.

2.2   The Need for Demographic Monitoring

Perhaps the primary reason why demographic monitoring, as opposed to population monitoring through periodic censuses, is especially important for seabird populations stems from their life-history characteristics, which are quite different to many other bird species (Fisher 1952; Gaston 2004). Most seabirds, despite living in often harsh environments, they have generally high (and not very variable) rates of survival, and thus a long lifespan; for example, some ringed Manx Shearwaters in Britain exceed 50 years of age. They have low rates of productivity; many species lay only one or two eggs, and individuals may not breed in every year, particularly amongst the larger species, and there can be a high degree of variability in breeding success between years. Young birds also have an extended immature period, with some individuals spending their first years at sea, not returning to colonies to breed until they are at least three, and in some as many as ten, years old. As a consequence changes in productivity and immature survival may take several years to feed through into population changes and so the effects of such drivers of change may not be seen in the population for many years. Impacts of changes in adult survival, on the other hand, will usually be seen in the immediately following years. However, in order to detect such changes it is necessary to have marked individuals as previously non-breeding mature individuals may replace breeders that fail to return to the colony resulting in little discernible change in numbers, particularly where only a portion of a colony is monitored. Thus for seabirds, perhaps more than any other avian taxonomic group, changes in demographic rates have the potential to provide an early warning of future population problems.

A second reason for demographic monitoring stems of seabirds, though not unique to this group, is the wide range of pressures their populations face. These include changes to food resources, both in the breeding and non-breeding seasons, for both environmental (*e.g.* climatic) and anthropogenic (*e.g.* overfishing) reasons, susceptibility of nests to introduced predators and direct anthropogenic impacts, such as pollution (notably oil-spills), accidental harvesting, habitat loss (primarily inland breeding species), and increasingly, potentially from onshore and offshore energy generation infrastructure. A further consideration is that changes in such factors are often less immediately apparent than changes in terrestrial ecosystems might be because they occur under water and/or far from land and so are hard to monitor directly. Determining which of these factors is affecting a population requires an understanding of demographic parameters, and the mechanisms whereby ecological drivers can affect them, in order to effectively draft management plans for mitigating or adapting to the population pressure.

Thirdly, seabirds, being at the top of most marine food chains can act as important bioindicators of the health of marine ecosystems (Furness *et al.* 1993). Understanding why and how seabird populations are changing can provide insight into mechanisms of population change elsewhere in the ecosystem. More generally, as noted above, the United Kingdom has obligations under a number of international instruments (notably the European "Birds" (EC/79/409) and "Habitats" (EEC/92/43) Directives, the Ramsar Wetlands Convention and the Agreement on the Conservation of Albatrosses and Petrels) to maintain the favourable conservation status of many of its seabird populations. In order to achieve this in an effective and cost-efficient manner, it is necessary to understand the demographic processes underlying observed population changes.

2.3   Britain's Seabirds and Current Demographic Monitoring

Britain and Ireland are two of the most important countries in Europe for seabird populations, with in excess of 8 million birds using our shores (Table 1). Seabirds can be defined as 'those species which spend long periods away from land and obtain all or most of their food from the sea while flying, swimming or diving' (Nettleship 1977; Gaston 2004). This utilisation of marine habitats has arisen independently at least four times over the course of avian evolution, with the Orders being

Sphenisciformes (penguins), Procellariiformes (albatrosses, petrels, storm petrels and diving petrels), Pelicaniformes (pelicans, boobies, tropicbirds, frigatebirds and cormorants) and Charadriiformes (auks, gulls, terns and skuas) all comprising mostly seabird species, though some birds from other orders, such as several species of duck (Anseriformes), notably scoters *Melanitta* could be considered seabirds. In this review we consider the species that formed the core of Seabird 2000 census (Mitchell *et al.* 2004), with the exclusion of Mediterranean Gull *Larus melanocephalus*, which is present only in small numbers at the northern edge of its (admittedly expanding) range. Britain and Ireland are particularly important for seabirds during the breeding season: many of the cliff-nesting species disperse out to sea during the non-breeding period, while some terns and skuas migrate to regions in the southern hemisphere.

Despite their diverse evolutionary origins, seabirds show remarkable similarities in their population ecology that have developed independently through convergent evolution to allow their populations to persist in temporally variable marine environments (Furness and Monaghan 1987). All species have high survival rates, generally between 80 and 95%, resulting in high longevity spanning decades (Croxall & Rothery 1991). All species also have a low fecundity characterised by a single breeding attempt, small modal clutch sizes (only one to three eggs in most species) and intermittent breeding by mature adults (Furness & Monaghan 1987). Breeding success tends to be on average low, and periodic breeding failures may occur due to variations in food availability (Hamer *et al.* 1991, Monaghan *et al.* 1992, Nur & Sydeman 1999). Juvenile survival is also low relative to that of adults (e.g. Wernham *et al.* 1997). All species exhibit periods of deferred breeding spanning three to fifteen years (Furness & Monaghan 1987). As a consequence of these characters, seabirds have long generation times, low intrinsic rates of population increase and relatively stable population trends.

Britain's seabirds can be categorised into a small number of functional groups, which broadly follow their taxonomic status (Table 1). Within each group, the species share similar traits and will be likely to require similar demographic monitoring protocols (Walsh *et al.* 1995; Mitchell *et al.* 2004). These groups are discussed in detail in later chapters. However, the nature of current demographic monitoring differs dramatically between groups: for some cliff-nesting auk species highly detailed annual information is available (although only from a small number of colonies), while for the burrow-nesting petrels very little is known.

In order to characterise the demography of seabird populations a minimum of four parameters are required: age-specific survival and productivity rates, age at first breeding and proportion of mature birds that breed in any given year (Croxall & Rothery 1991). Of these, three are required on an annual basis, while the age of first breeding is often considered to be characteristic of a population and largely unchanging through time, though in practice there is likely to be variation between individuals. Similarly, in some cases one might be able to (or have to) assume that a similar proportion of individuals breed in each year. Of course, information on age at first breeding or average numbers breeding each year is likely to come from demographic monitoring programmes too.

Periodically, a complete census of Britain and Ireland's seabird populations is attempted (Cramp *et al.* 1974; Lloyd *et al.* 1991; Mitchell *et al.* 2004). In between these censuses, annual monitoring of numbers at selected colonies is undertaken and, since 1988, co-ordinated by the Seabird Monitoring Programme (SMP). Most of the available information on trends in numbers was presented in detail by Mitchell *et al.* (2004) and will not be considered further here, rather we focus on demographic monitoring, i.e. monitoring of survival rates and breeding productivity. Information on breeding productivity at a limited number of sites is collected through the SMP (Mitchell & Parsons 2007) and some information is also collected through the British Trust for Ornithology's Nest Record Scheme (Crick *et al.* 2003). Information on survival is derived from birds ringed as part of the British and Irish ringing scheme (Wernham *et al.* 2002; Balmer *et al.* 2008), with the SMP key sites of Canna, Fair Isle and, especially, Skomer and the Isle of May providing substantial amounts of data. Some degree of annual reporting on population size and breeding success is attempted (e.g. Mavor *et al.* 2006), but routine reporting of survival rates has not yet been attempted.

This report has three sections. We first briefly consider the availability of productivity data for seabirds, this was recently considered in more detail by Mitchell & Parsons (2007) so we largely summarise their findings (Chapter 2). Secondly, we discuss the availability of data on survival rates (Chapter 3). Because there is no formal monitoring programme for survival rates, we discuss some of the issues surrounding survival rate estimation and review data availability for each species, along with some of the challenges that might be associated with monitoring survival rates. Finally, in Chapter 4, we consider the potential for developing an integrated framework for monitoring seabird demography.

3.   DEMOGRAPHIC MONITORING: PRODUCTIVITY

As a group, seabirds are adapted to exploit an environment that is highly variable in terms of foraging resources, but rather constrained in terms of breeding sites. Thus they tend to be long-lived, with high survival rates between years (at least amongst breeding age birds), while productivity varies markedly from year to year in relation to food availability. Perhaps the extreme examples of this strategy are the larger albatrosses, individuals of which can live for several decades, but breed only every second or third year (e.g. Wiemerskirch 1992). Because breeding success is closely correlated with food availability, productivity can vary enormously on an annual basis, with complete failures in some years, notably recently for many species in the northern North Sea that rely on sand eel *Ammodytes* stocks (Frederiksen *et al.* 2004a).

3.1   Seabird productivity

Productivity of seabirds can be split into three components: the number of eggs laid by an individual; the proportion of those eggs that hatch and produce fledged chicks and the number that recruit into the breeding population. In many ways, it is the latter component which is the more important demographic parameter, *i.e.* in determining population size and change. This recruitment rate reflects a combination of the number of young fledged and pre-breeding survival. In seabirds this can cover a period of anywhere between three and nine years, depending on the species (longer in the larger species). Survival of birds in the years before breeding is generally lower than survival when a bird has reached breeding age, but quantifying these survival rates is extremely difficult since most seabirds disperse into offshore waters at this time, where few marked birds are observed. New technologies may help in this regard, but are likely to be relatively expensive; these and other issues concerning survival rates are discussed further in Chapter 4. As with many other species, survival of immature birds, and hence rates of recruitment, represents a key unknown in our demographic knowledge of seabirds.

As might be expected of long-lived birds, seabirds tend to have a relatively low productivity. All seabird species have small clutch sizes, typically only one (petrels, auks, gannet) or two to three (divers, gulls, terns, cormorants). Although there is some individual variation in the number of eggs laid (in those species that lay more than one), at a population level clutch size can reasonably be considered to be fixed. Without exception, all the seabirds considered here have a single breeding attempt each year, though some will re-lay if the initial attempt fails at an early enough stage. There may, however, be variation in the number of adults of breeding age that attempt to breed each year, with up to 30% (or more) of individuals not breeding in some years if environmental conditions are not suitable (*e.g.* Calladine & Harris 1997).

3.2   Monitoring seabird productivity

Clearly, in an ideal world, one ought to monitor the productivity of all individuals in a colony, or at least a random sample thereof. However, in most cases this will not be possible as typically topography and other factors will mean that only a section of the colony may be monitored. Some care thus needs to be taken in choosing which section to monitor, as productivity is likely to vary spatially within the colony, both in response to environmental variation (e.g. likelihood of predation) and to the quality of individuals breeding there. In many cases it may be necessary (and sufficient) to monitor the number of young (in aggregate) produced by individuals breeding in a delineated section of the colony.

Measuring productivity is often labour intensive, requiring multiple visits to the colony, particularly for species where the timing of breeding exhibits a marked degree of asynchrony (such as Shag), so tends to be undertaken at a limited range if colonies (Table 2), particularly sites where there is at least some degree of professional involvement. Much of this information is collated by the Seabird Monitoring Programme, but some is also collected through the BTO Nest Record Scheme and information on terns tends to be collated by the RSPB, since a large proportion of several populations

occur in their reserves. Monitoring tends to be more thorough for the scarcer species which breed in a limited range of colonies. Data collated by these schemes tends to be at the site level, *i.e.* productivity of individual pairs is not generally identified (although it may be collected). Such a level of detail is generally sufficient for monitoring purposes and an understanding of how productivity changes through time in relation to different environmental factors in determining changes in breeding success.

The ease of monitoring breeding success differs between species groups, and largely relates to how easy it is to count the chicks and relate these to particular individuals or pairs (Walsh *et al.* 1995). Fulmar and Kittiwake are probably the easiest species to monitor, in that pairs generally nest in relatively discrete and identifiable sites, which are often visible from a land-based vantage point. Other gull species, skuas and terns represent more of a challenge because shortly after hatching their chicks leave the nest, making it difficult to attribute individual chicks to a specific pair.

Cormorants and Shags also make distinct nest-sites, though these sites may be fairly difficult to count because of their location, particularly in the case of the Shag, which will often nest on ledges in sea-caves or among boulders at the foot of cliffs, for example. An additional challenge is that nesting attempts are asynchronous, so that in a single colony, different nests may be at very different stages with some containing newly-laid eggs whilst others contain chicks about to fledge. This means that monitoring breeding success of shags and cormorants requires many more visits to the colony compared with species that breed more synchronously.

Measuring breeding success of some burrow- and crevice nesters (*i.e.* storm-petrels, shearwaters, razorbills and black guillemots) is extremely difficult because of the inaccessibility of nest sites. Puffin burrows have, however, generally proved easier to investigate. Monitoring breeding success of cliff-nesting auks, such as guillemot, is also difficult because they do not build a nest but simply lay their single egg on bare rock, often on crowded ledges which may only be visible from an offshore vantage point. Following the fortunes of individual breeding pairs without easily identified nest sites requires intensive study involving many repeated visits and can be very time consuming.

As with any demographic parameter, there is likely to be regional variation in breeding success, dependent on local factors, notably food availability (e.g. Frederiksen *et al.* 2006). For example, Parsons *et al.* (2007) demonstrated regional variation in breeding success in nine species – Fulmar, Shag, Cormorant, Great Skua, Kittiwake, Common and Arctic Terns and Guillemot. There was no significant regional variation in breeding success of Arctic Skua and Little Tern; and data were too sparse for any regional trends to be discerned for Manx Shearwater, Sandwich Tern, Razorbill and Puffin.

Coverage for many species is adequate to produce representative national indices of breeding success (Mitchell & Parsons 2007), while coverage for other species is noticeably lacking, *e.g.* Herring and Great Black-backed Gulls and Razorbill (Table 2). Given the practical difficulties in assessing productivity of burrow and crevice nesters, it is perhaps unsurprising that data are scarce for the petrels, Black Guillemot, and even Puffin. However, in order to effectively monitor the impacts of changing environments on breeding success it will usually be necessary to monitor breeding success regionally as different drivers are likely to operate in each area. A useful way forward, particularly when it comes to assessing the threats to coastal and marine ecosystems, is the use of indicator groups of species, with particular species being chosen to reflect processes in the wider environment (Way & Mitchell 2008).

4. DEMOGRAPHIC MONITORING: SURVIVAL

Studying survival requires following marked individuals through time. This is usually done by fitting birds with uniquely numbered metal or coloured leg ring. Because of their life-history, birds are usually caught and marked during the breeding season, either as chicks or breeding adults; with a relatively small group of colonies accounting for a large proportion of marked birds (Table 3), however, their colonial nature means that large numbers of seabirds are available to be captured and marked within a small area. Capturing chicks, at least for non-cliff-nesting species is often a matter of simply picking birds up out of nests or the ground; adults can sometimes also be caught with nooses, nest traps, mist nets and hand nets with varying degrees of difficulty depending on the species. Most birds are ringed as chicks because relatively large numbers can be ringed with minimal disruption in colonies which may be sensitive to disturbance. Full-grown birds are also ringed in some colonies, either on particular study plots, or more generally, often on the edge of the colony. Away from the nest it can be difficult to distinguish breeding and non-breeding birds, particularly for oceanic species like petrels, and there is no guarantee that a bird caught at a colony is breeding there, even if it has a brood patch (Insley *et al.* 2002). Amongst colonial seabirds, relatively few birds are ringed away from the breeding colonies; a high proportion of those that are being associated with oil spill incidents and therefore do not provide representative data for population monitoring. Most gulls are ringed away from the colony, typically on the colony at landfill sites, however, many of the larger gulls are fitted with colour rings, so can be relatively easily observed when they attend their breeding colony.

Because seabirds are long-lived, as discussed earlier, it is important to distinguish between survival of immature and adult birds. The probability of immature birds surviving a given year is typically much lower than that of an adult bird, but it is likely to increase with age (there is little evidence survival changes substantially with age amongst all but the oldest adults). Survival of immature birds is perhaps the hardest demographic parameter to measure since most immatures disperse from their natal site, in contrast to adult birds, which often exhibit a degree of site philopatry (discussed below). It is particularly hard to estimate age-specific survival in seabirds as immatures of many species spend a substantial proportion of their time offshore, where there are few observers to encounter them. In many cases it may be more appropriate simply to estimate overall survival from fledging to breeding age, which is the key quantity demographically.

Survival rates can be estimated from either the number of times individuals are re-sighted, or from knowing the time of death. Initially, methods for these two types of data were developed largely independently (Williams *et al.* 2002), but since the models underlying survival estimation in each case are similar in form (*i.e.* product-multinomial) methods have been developed to combine information from both sightings of live birds and recoveries of dead birds in survival rate estimation (e.g. Barker 1997). Estimation of survival probabilities for seabirds is particularly difficult, so below we provide a general discussion of some of the main assumptions required before going on to discuss the availability of recent estimates of survival rates for each species. A key factor is determining the success of such analyses is consistency of effort and planned sampling to improve homogeneity in capture likelihoods of individuals. Although the methods for survival rate estimation from live recaptures and dead recoveries share underlying similarities, different assumptions and biases are involved in estimating survival rates from live sightings and from dead recoveries. So we shall discuss the two methods separately before outlining methods to combine them.

4.1 Mark-recapture methods

Mark-recapture methods estimate survival from observations of live individually marked birds. 'Capture' events may involve physically re-capturing the bird or resighting field-readable rings fitted to a free-ranging bird, and we will refer to both types of event as 're-captures'. Most often re-capture or re-sighting events occur during the breeding season when the bird is attending a colony, effectively creating annual sampling occasions. Effective sampling of individuals requires a high degree of effort and is usually undertaken by a team of dedicated volunteers working in a particular colony or professional fieldworkers.

Estimation of survival rates over a specific period of time from mark-recapture data requires the simultaneous estimation of the probability that the bird is re-captured (or re-sighted) during the period to account for birds that are alive, but simply not detected (Lebreton *et al.* 1992). Analyses to estimate these probabilities have been developed around the Cormack-Jolly-Seber (CJS) model (Cormack 1964, Jolly 1965, Seber 1965). This was initially devised to allow estimation of population size in open populations, in which survival and recruitment were a by-product and recapture rate a nuisance parameter. More recent developments of this method have focused on estimating survival rates and determining the effects of external and intrinsic factors upon it (Williams *et al.* 2002).

Accurate estimation of survival rates using Cormack-Jolly-Seber models depends on the following set of assumptions:

1. All marked individuals in the population are equally likely to be captured on any given sampling occasion.
2. Each individual within the population, or identifiable subpopulation (such as age- or sex-specific group), has the same likelihood of surviving from one sampling occasion to the next.
3. Marking events are instantaneous, or at least short in duration relative to the period over which survival is measured.
4. Marks are not lost or overlooked.
5. Emigration does not occur, or is measurable.

For most seabird populations, these assumptions are not met to a greater or lesser degree, we discuss the importance of each in turn.

4.1.1 Equal capture rates

Because seabirds are generally highly colonial, sampling sites (at the level of the colony) are relatively easily defined for most species. A large number of birds are available within a relatively small area which allows large marked sample size and high re-capture rates, combining to produce a high precision in the survival estimates that would be hard to attain in more dispersed species. However, within a colony capture (and re-capture) probabilities can vary enormously with the location of the breeding site, which may be easily accessible/visible, or completely inaccessible/invisible; this will tend to co-vary with the birds age, status and condition (Green 1995, Spendelow *et al.* 1995, Harris *et al.* 1997a). Studies that rely specifically on re-trapping seabirds to read their BTO ring rather than re-sighting their colour rings, may create problems of trap-avoidance rather than trap-happiness, though careful study design can help to minimise these problems in some cases. Conversely, adult seabirds often exhibit high micro-site philopatry, returning to the same nest site or territory, rather than settling randomly in the colony, each year. Thus, spatial variation in re-capture rates due to methodology or differences in behaviour among birds may make some more likely to be re-captured than others, and, particularly, that birds captured recently are more likely to be re-captured than those that were not (birds are effectively 'trap-happy'). Behavioural differences can also result in unequal capture rates, for example, females often incubate more than males and so will be more likely to be (re-)captured (*e.g.* Prévot-Julliard *et al.* 1998), or birds may only breed intermittently (*e.g.* Calladine & Harris 1997). These problems are particularly marked for cliff-nesting seabirds, such as auks, but probably apply to varying extents in all seabird species. Thus, the limits of the study population and the sampling strategy within it need careful definition.

Severe capture heterogeneity is most likely to result from spatial variation in capture effort. To avoid this it is imperative to ensure the per-capita search effort for marked birds is similar throughout the colony or study site. A record of effort for each sub-area in the study site or colony should be maintained during fieldwork to ensure each section receives similar effort. Recording the sub-area birds are seen in can allow spatially dependent re-capture rates to be estimated in the event of heterogeneity occurring, but this will be at the expense of precision in survival estimates and power to detect factors affecting it (Frederiksen & Petersen 1999). Behaviourally induced differences in re-

capture rates among individual birds and temporary emigration are more difficult to deal with. Individual covariates, such as age or sex, which may account for heterogeneity should be collected where possible so separate estimates of re-capture rates can be calculated. Temporary emigration effects (birds moving to breed at other colonies or taking years off breeding at sea) can only be dealt with statistically by producing re-capture estimates that are dependent on whether or not birds were seen in the previous year (Pradel *et al.* 1993, Harris *et al.* 1993, Ratcliffe *et al.* 2008).

4.1.2   Equal survival rates

A key assumption of the CJS methods is that survival rates of individual birds in particular groups within the population is equal. This is almost certainly not true in most cases. Perhaps the most notable deviation from this assumption is that of constant survival with age. It is well known that in seabirds, as in many species, survival varies with age. In general, survival increases until breeding age but remains broadly constant thereafter though, as they are so long-lived, a senility effect has been detected in some species, with survival decreasing towards the end of their lifespan (e.g. Reed *et al.* 2008, though see Nisbet 2001). In principle this can be accounted for by including age as a covariate in the models, though this obviously requires multiple cohorts of birds (particularly where year/time specific survival rates are being estimated), and birds of known age. Survival tends to be lowest, and most variable, in the young birds under breeding age. Of course, these are the birds that are least likely to attend to the colonies and hence about which information is scarcest. Age specific variation in survival can, in principle at least, be accounted in the estimation procedure by including an age variable, or grouping birds into different age-classes.

4.1.3   Marking is instantaneous

A central assumption of mark-recapture modelling is that the period of marking is instantaneous, or at least very short relative to the period between capture intervals. This is essentially because these models assume there is no mortality during the marking period. For seabirds almost all marking is during the breeding season, a period which is relatively short (*c.* 2 months) relative to the period between breeding seasons. Additionally survival (of breeding adults) for most species during the breeding period is likely to be very high, meaning mortality will be minimal; a possible exception to this may be species like Leach's Petrel, which can suffer extremely high predation pressure (Phillips *et al.* 1999). Where mortality during the period is thought to be significant, models based on the 'robust design' which allow modelling of survival rates from repeated samples during the breeding season, as well as between breeding seasons, may be worth considering, though they are likely to be applicable in only a few instances as they require much data to estimate all the required parameters (Williams *et al.* 2002).

Survival rate estimates are, however, moderately at least, robust to violations of the assumption of instantaneous marking (Smith & Anderson 1987; O'Brien *et al.* 2005). Providing there is no systematic change in the pattern of ringing effort, and the period of ringing is reasonably short compared to the period over which survival is estimated then any bias in estimating survival rates should be small.

4.1.4   Marks are not lost

Mark recapture models actually study the survival rate of the marks fitted to animals rather than the animals themselves. To avoid underestimating survival rates, marks fitted to them must be permanent or the loss rate must be estimable. Seabirds have a very high longevity and so marks must be very durable to allow for this. Rings fitted to seabirds are also subjected to a high degree of wear due to exposure to corrosive salt water and guano, exposure to UV light and mechanical abrasion on rock, sand and soil. This may result in rings being lost altogether, inscriptions becoming illegible, colours fading or rings slipping into one another so only one is visible (e.g. Spendelow *et al.* 1994). Rings made of incoloy (a nickel-chromium alloy) and stainless steel were introduced in the late 1970s (replacing monel). These are very durable, but given the longevity of seabirds even these sometimes

need replacing, particularly in species that nest on rocky ledges or in crevices (such as auks), where the ring may be exposed to considerable wear. Complete loss of metal rings is unlikely to be a serious problem for most seabird species.

Problems of ring loss are likely to be greatest where colour rings are re-sighted, as even UV-stable plastics (such as certain forms of Darvic) can degrade over time. Marking with two or more rings or marks is essential to estimate or correct ring loss (Becker and Wendeln 1996). Multiple ringing is typical of most resighting studies, involving a BTO ring in conjunction with a special ring or a combination of three or more colour-rings. In these instances, birds that have lost or worn rings can usually be identified based on those rings that remain. The best remedy for partial colour ring loss is recapture and replacement as soon as the ring loss is detected, where possible. As the likelihood of all colour rings being lost over a single year is extremely low, prompt replacement should ensure that loss of birds from the study population will be largely due to mortality or permanent emigration. As metal rings are unlikely to be lost, an assessment of the severity of the problem can usually be made and is likely to be greatest amongst cliff-nesting species, where birds are continually shuffling along cliff-ledges. A possibly significant source of ring-loss occurs in terns where rings may be removed by trappers on the wintering grounds, particularly in west Africa (Becker & Wendeln 1996); we discuss this in the relevant section below.

4.1.5   Emigration is negligible

As mark-recapture studies usually focus on a relatively limited area (in this case usually the focal colony or colonies) permanent emigration away from the site cannot be distinguished from mortality. Temporary emigration can be accommodated (although it reduces the apparent re-capture rate), but may create heterogeneity in the capture rate between individuals; perhaps most commonly as birds avoid the area of marking/recapture for a period following capture (trap-dependence). This leads to a distinction between estimates of 'true' survival, where emigration is completely accounted for, and 'apparent' survival, which includes an element of permanent emigration and so is lower than the 'true' survival. In species with high site fidelity (as for many seabirds of breeding age) the amount of emigration may be low, so apparent survival may approximate true survival, but this need not be so. Studies of colour-marked birds usually calculate apparent survival, whereas information from dead recoveries (which may be found anywhere) is usually required to estimate true survival.
As with many species, survival rates of immature seabirds cannot usually be estimated accurately using re-captures as natal dispersal among colonies occurs between fledging and recruitment into the breeding population (Nisbet & Drury 1972, Nichols 1992). Surviving birds may either never return to the natal colony or prospect there transiently before occupying an alternative colony (e.g. Furness & Baillie 1981). Local recruitment models for live-recapture models have been developed and applied to seabirds (Pradel & Lebreton 1999, Oro & Pradel 2000), but in most seabirds these will produce an underestimate of survival to breeding age unless the geographic distribution of the study species is confined to a single colony.

Once seabirds have selected a site at which to breed, they usually exhibit extremely high site fidelity, to the degree that most species return to the same territory or breeding site within a colony each year (e.g. Harris & Wanless 1989, Harris *et al.* 1997a, Phillips & Furness 1998, Catry *et al.* 1998). As losses due to emigration are negligible, apparent survival estimated from re-captures are likely to be close to true survival rates. However, site fidelity by breeding birds is not a universal rule in seabirds: breeding terns may move among colonies in response to predation, disturbance and changing habitat or food supply, so studies of tern survival at single sites may produce underestimates owing to emigration (Nisbet and Cam 2002, DiCostanzo 1980, Spendelow *et al.* 1995, Ratcliffe *et al.* 2008).

4.1.6   Summary

Collecting data on live re-sightings of birds usually yields much more data than relying on recoveries of dead birds, although it can only provide information on return rates to the colony. So, ideally, such studies should be done in conjunction with analyses of dead recovery data, either separately (4.2) or

jointly (4.3). In many cases, philopatry of adult seabirds is high, so even local return rates can yield useful indications of patterns in adult survival probabilities. As discussed above, estimation of survival probabilities for immature birds is much more difficult, and is probably impossible from colour-ring studies alone.

Observers should always be alert to problems of ring loss, particularly when undertaking colour-marking studies, which is likely to be more of a problem for seabirds than many other groups given their longevity and the adverse environments in which they live. With careful consideration such problems can be minimised, or at least the extent of the bias assessed. Similarly, providing there is little systematic change in ringing effort, the bias introduced by ringing over a breeding season, rather than instantaneously, should be small.

A greater problem is the existence of heterogeneity as this can seriously bias estimates of survival rates (particularly where there are changes over time) as well as introduce difficulties in the estimation process, e.g. through model convergence (Robinson *et al.* 2007). Wherever possible, sources of heterogeneity (e.g. different ages, populations, wintering areas) should be identified and a steps taken to control or eliminate (by selection of appropriate data subsets) them. The best mechanisms for doing so, however, are likely to be specific to particular studies.

4.2   Mark-recovery methods

The coloniality of seabirds allows the ringing of a large number of birds within a small area, and a large number of seabirds have been ringed over the last 30 years. In contrast to mark-recapture methods, mark-recovery analysis of birds relies on two sampling occasions: when the individual is marked and when it is recovered (found) dead. Individuals can also be recovered dead at all ages and, potentially, anywhere within their bio-geographic range rather than solely at study colonies.

As with mark-recapture analyses, it is necessary to estimate a 'nuisance' parameter, the probability of recovery, to measure the probability that a dead bird is found shortly after death, *and* that the mark is reported to the scheme co-ordinator (i.e. BTO for birds ringed in Britain). Recovery of dead marked birds may occur globally, and corpses of seabirds are usually found either by members of the public or by response teams dealing with oil spills, or other environmental incidents. Dead recovery data can therefore be used to estimate pre-breeding survival rates as well as those of adults as they allow age-specific survival prior to recruitment into the breeding population to be examined and emigration is not a confounding variable. They provide information on survival over a wider geographical range than mark-recapture data and can also produce other data that can be useful in diagnosing population declines, such as migration routes, wintering areas and causes of death (Harris and Tasker 1999; Wernham *et al.* 2002).

Early analyses of metal ring recoveries mainly covered descriptions of distribution and longevity records (e.g. Thomson 1953, Harris 1964), or were based on life table models of survivorship (e.g. Bellrose & Chase 1950, Hickey 1952, Anderson 1981). In 1951, Lack described a method for estimating mortality directly from the return of rings on dead birds. However, this method was only applicable when all the birds ringed as nestlings in a given year had died, creating considerable problems for long-lived seabirds. Haldane (1955) extended this method to allow the use of 'incomplete' data, applying a maximum likelihood correction for unavailability of marked birds that remained alive. This multinomial model, similar in form to the CJS model for mark-recapture data saw much development in the 1970s and 1980s to account for varied circumstances (e.g. Brownie *et al.* 1985, North 1987).

The use of ring recovery data for the accurate estimation of survival rates is dependent on the following assumptions.
1. Random sampling (with equal probability of return of marks from all birds dying).
2. Equal survival probability for all marked individuals (independent of age and sex), or knowledge of these parameters for individuals so they can be modelled as covariates.

3. No loss of marks (or marks over-looked).

The issues regarding the latter two assumptions are much the same as for mark-recapture data (see above). However, because recovery analyses integrate survival information over larger areas, there is likely to be spatial heterogeneity in survival rates between colonies. Clearly, the probability of an individual surviving will vary depending on the environmental conditions encountered; these are likely to vary to at least some extent between colonies. Given that seabirds spend such a large proportion of their time at sea, and that this is likely to be where most mortality occurs, it may be sufficient to determine groups of colonies for which survival probabilities of individuals in them are likely to be similar. In this regard, statistical similarity (i.e. insufficient evidence of a difference) is likely to be all that is possible to achieve as, in almost all cases, it is unlikely that there will be sufficient analytical power to detect small differences in survival probabilities. Because of data constraints survival probabilities have typically been calculated for one or a very few intensively studied colonies, or over very large areas; characterising regional variation in seabird survival will be a key challenge for the future. Notwithstanding this, if mortality is expected to occur during the interval between sessions, i.e. during migration and winter, similarity of survival among colonies can be inferred to some extent as implying similarity in wintering areas.

4.2.1   Variation in reporting rate

A major consideration for mark-recovery data comes from unequal recovery rates, both temporally and, particularly, spatially. Most obviously, the locality at which a banded bird dies relative to human population density will influence the likelihood of its recovery. Seabirds spend a large proportion of their lives at sea far from land so the majority of corpses simply sink and are never washed ashore (Bibby & Lloyd 1977, Bibby 1981, Flint & Fowler 1998). Therefore the recovery rates of seabirds tend to be low; generally fewer than 5% of all seabird rings are ever recovered, although this may be higher in species that are culled (e.g. cormorant). This low average recovery rate is compounded by declining reporting rates in recent years (Robinson & Grantham in press).

The geographical location at which a bird dies has a large influence upon its likelihood of being recovered and reported. Most seabirds disperse into offshore waters during the non-breeding season; any that die naturally at sea will sink and be unrecoverable, only those washed ashore or dying at their colonies will be available to be recovered. The likelihood of a seabird that is on the shore being found depends on the human population density and the topography of the coastline. Birds are more likely to be found on sandy beaches than rocky or estuarine coasts as dead birds are easier to distinguish from the substrate and people tend to walk along sandy coastlines more often. There are also variations in the likelihood of a bird corpse that has been found being reported resulting from cultural and social factors such as literacy, education and environmental awareness. All these factors combine to produce highly heterogeneous likelihoods of dead birds being reported according to geography, and this introduces biases into the survival estimates if reporting rates are assumed to be constant across the species range.

Cause of death varies among seabirds and this may affect their likelihood of recovery. Most birds will die of natural causes such as starvation, but some are caught and drowned in fishing gear (driftnets or longlines), shot, deliberately trapped or oiled. These latter causes of death are more likely to bring the corpses into contact with humans and so they are more likely to be recovered and reported. The chances of a dead bird being reported will therefore vary in relation to the spatial distribution of these mortality factors within the species geographic range.

If all birds in a population moved randomly in relation to the factors described above, the likelihood of an individual being reported would be homogenous and the assumptions of the survival models would be met. However, populations of seabirds around Britain and Ireland often have discrete distributions that exhibit little overlap. A bird dying during the summer is most likely to be recovered at the colony at which it was ringed (especially if ringed as an adult) or within a region comprising the meta-population within which the bird was hatched (if ringed as a chick). Different populations of

seabirds around Britain can also occupy discrete wintering grounds. If factors such as human population density, shoreline type and mortality factors vary among these largely discrete summer and winter distributions, reporting rates will be dependent on the location at which a bird was ringed. This will create biases in survival rates in analyses assuming spatially constant reporting rates. In species for which large samples of ringed birds are available, it may be possible to circumvent such problems by modelling region-specific reporting rates.

The other main factor affecting seabird distribution and mortality causes is its age. Birds in their first winter often have a wider distribution than older birds (Wernham *et al.* 2002). In summer, adults return to the colonies whereas immature birds generally remain in the wintering grounds for one or more years. Immature birds also tend to be more susceptible to being trapped or shot than adults, which makes it more likely that their corpses will be recovered (e.g. Heubeck *et al.* 1991, Harris *et al.* 1997*b*). These differences in distribution relative to the likelihood of a dead bird being reported create heterogeneity of reporting rates among ages. Differences in reporting rates among ages create serious problems in age-specific survival estimation for seabirds because most individuals are ringed as chicks (Clark *et al.* 2006). Adult survival rates can be estimated robustly from nestling-only data, but biases arise in estimation of immature survival because it is necessary to assume reporting rates do not vary with age (Anderson *et al.* 1985). These biases vary from small and 'acceptable' (Freeman & Morgan 1992, Rinne *et al.* 1990, Catchpole *et al.* 1998) to large and 'unacceptable', (Anderson *et al.* 1985, Francis 1995, Catchpole *et al.* 1995) depending on the species age-specific distribution and mortality factors. Investigation of the biases in immature survival rates caused by assuming constant reporting rates with age is needed for seabirds, using species for which the data are adequate to estimate age-specific reporting and survival rates (e.g. Guillemot). Interestingly, Wanless *et al.* (2006) were able to estimate age-specific survival rates in gannets by fitting a more complex model with time-dependence in the survival rates; whether this will be generally true is unknown. However, robust estimates of immature survival rate for most species in the future are likely to depend on ringing adult and subadult seabirds or through joint analyses incorporating re-sighting rates of birds ringed as chicks (i.e. of known age).

Long-term studies of recovery data also need to take into account that reporting rates can (and do) change with time. For example, shooting pressure has reduced with introduction of protection laws, for example, Cormorants have been legally protected in Ireland since 1976 and in Britain since 1981 (Wernham & Peach 1999); changes in the fishing industry affect the by-catch of auks and other seabirds; the severity of chronic and episodic oil pollution is also variable over time (and awareness of pollution may increase vigilance and reporting rates on beaches). There is also evidence for a long-term decline in reporting rates for rings in general (Robinson & Grantham in press). Modelling time dependence of recovery rates in long-term studies of survival rates is clearly essential to obtain reliable estimates of trends in survival through time.

4.2.2   Summary

Robust estimates of survival rate are likely to depend on complex modelling of recovery rates in relation to time, space and age to minimise biases. Generating regionally specific estimates of survival rates is likely to require focussed and consistent ringing at a sufficient number of suitable sites, however given the current distribution of ringers, this will require significant extra effort and training.

The quality of the dead recovery data is highly variable among species, so only for some species is it likely to be possible to produce robust estimates of survival rates to facilitate diagnosis of population declines. More work is required to characterise the spatial pattern of recoveries and how this might have changed over time to fully assess how these might influence survival rate estimates. It is likely that combining mark-recovery with mark-recapture (see 3.3) or other population information (see chapter 5) will allow patterns of survival to be modelled in more species than using just the mark-recovery data alone.

4.3   Joint survival models

The two major classes of models for analysing survival rates (mark-recapture and mark-recovery) have different strengths and weaknesses as described above. Mark-recapture studies generally provide estimates of higher precision, but are restricted in their spatial scale. There is no practical way of separating permanent emigration from death so that estimates of survival rates from mark-recapture (or mark-resight) studies can only be considered a minimum (*i.e.* a return rate), and it is not possible to estimate juvenile survival compared with that of older birds because this is confounded with large-scale dispersal and delayed maturity. Mark-recovery studies, on the other hand, tend to provide lower precision estimates from a larger scale, but can give information on the survival of immature birds (Lebreton *et al.* 1992). In many cases, there may be an insufficient number of recoveries to estimate annual survival rates, rather years may need to be combined, or related to a covariate. Since both mark-recapture and mark-recovery models are based on similar statistical structures (usually product-multinomial in form) it is natural to consider a fusion of the two approaches where data allow (Catchpole *et al.* 1998; Barker 1997).

Burnham (1993) developed a model for the joint analysis of mark-recovery and mark-recapture data for discrete studies in which all animals are exposed to both forms of re-capture. An example of this would be an intensive study on a single island with birds ringed there being both re-sighted alive and reported dead. Lebreton *et al.* (1995) developed models that utilised both forms of capture history to estimate common parameters for studies based on different groups of animals. An example of this approach would be the integration of an intensive colour-ringing study of a seabird species at a single colony with dead recoveries of non-colour ringed birds from that and other colonies. Barker (1997) further generalised Burnham's models to allow re-sightings, recaptures and recoveries to be modelled jointly. These models assume that all birds in the population share similar survival probabilities. This precludes analysis of age-specific survival estimates that is necessary to determine juvenile and immature survival rates as well as those of adults, although recent developments (Barker 1999, Ratcliffe *et al.* 2008) mean such models are becoming feasible.

Relatively few studies have applied the joint recovery-recapture approach to seabirds successfully. Catchpole *et al.* (1998) successfully estimated age-specific survival rates of Shags ringed on the Isle of May using a derivation of Burnham's (1993) method. After ringing, birds were either re-sighted alive on the May during the breeding season, or recovered dead elsewhere at other times. In this case, all the birds marked in the study could be recovered or re-sighted over the same time period, which minimised heterogeneity among the data sources. The integration of live re-sighting data of adult Great Skuas on Foula during a relatively short study with dead recoveries of non-colour-ringed birds from that and other colonies over a longer term failed to produce robust survival estimates due to heterogeneity in the different data sources (SN Freeman pers comm). Further evaluations of the application of these methods to estimation of age-specific seabird survival rates are needed, as does the alternative approach of combining these data with others in a population framework.

4.4   Summary of recent survival estimates in seabirds

In this section, we summarise previous studies of the survival rates of each species. We have grouped species into broad ecological and taxonomic groups, as many of the issues related to survival estimation are similar for species within these groupings. The study of seabirds, particularly by colour-marking individuals has a long history, especially in Britain, with population studies on some colonies, such as Skomer and the Isle of May (both SMP key monitoring sites), going back many decades. Inevitably, early estimates of survival rates from these studies used relatively simple calculations that were unable to fully account for heterogeneity in survival or reporting rates. Where possible, we have limited the discussion to more recent studies where this heterogeneity has been taken account of, at least to a certain extent. We have also largely focussed on estimates from Britain (and Ireland), but have included a few studies from elsewhere where this seemed appropriate.

Discussion for each species follows a more or less standard format, starting with a brief introduction to the species in terms of population status and life-history characteristics that are likely to be relevant to estimating survival. We then present information on publications reporting recent estimates of survival rates, before critically evaluating the availability of current data to estimate survival rates.

4.4.1   Cliff-nesting seabirds

4.4.1.1 Fulmar

Introduction

Fulmars are one of the commonest seabird species in Britain, having increased in numbers enormously during much of the 20th Century and colonising many new areas. However, in recent years the rate of increase has slowed markedly, and at some the biggest colonies, small decreases in numbers have been seen (Mitchell *et al.* 2004). They are Amber listed (Eaton *et al.* 2009), but only because most of the population occurs in fewer than 10 colonies. Fulmars are widespread around Britain and so a large number of colonies at which survival studies could be conducted exist. Their nesting habitat is mainly cliffs, but they will use grassy ledges on low, sloping cliffs on islands and so are on the whole more accessible than other cliff nesting species.

Summary of recent estimates

Fulmars are among the more easily studied of seabirds, having well-defined nests and with at least some populations nesting on accessible cliffs. There has been a long-term colour-marking programme of Fulmars on Eynhallow in Orkney since 1950 and a number of papers have reported on the findings of this study (e.g. Dunnet *et al.* 1979; Grosbois & Thompson 2005), which has yielded robust estimates of apparent survival rates, from re-sightings of colour-marked birds at the colony. A total of 115,000 birds have been ringed, but with a relatively low recovery rate typical of seabirds (1.4%). Reasonable numbers of adults and juveniles are ringed, so it should be possible to estimate pre-breeding and adult survival rates, though the precision of these is likely to be less than that obtained from colour-ringing.

Issues for estimating survival rates

Natal philopatry is low, so we would be unable to obtain estimates of pre-breeding survivor-mark studies, but 90% or more of adults return to breed at (or near) the same site each year (MacDonald 1977, Ollason & Dunnet 1978), meaning estimates of adult survival may be reasonable, at least for comparative purposes. The high site faithfulness of breeding birds means emigration will be minimal and the apparent survival rates resulting from live re-sighting studies will be close to true survival rates. Dunnet & Ollason (1978) recorded a significantly reduced probability of return in the year following ringing in fulmars, and this was especially so for new recruits; this will lead to trap avoidance responses in the re-sighting data although this can be modelled by including time-since-marking in the survival estimation. Hatch (1987) recorded that only about 5% of experienced birds failed to breed each year (due primarily to the physical destruction of their breeding sites or mate-loss). These birds would be unavailable for re-sighting if they left the colony and this could also create heterogeneity in re-sighting rates.

Fulmars are mainly pelagic outside the breeding season (Wernham *et al.* 2002), and only 1.4% of rings have been recovered. Although breeding adults and potential recruits tend to occupy the same areas in winter (within a few hundred miles of the breeding colonies) and thus will be subject to the same conditions, younger birds (1-4 year olds) tend to range much further (Dunnet *et al.* 1979). This creates marked age-specific variation in recovery rates which

means estimating pre-breeding survival rates will be difficult owing to a high proportion of birds being ringed as chicks, ideally more adults should be ringed to circumvent this.

4.4.1.2 Gannet

Introduction

The breeding Gannet population of Britain and Ireland is around 260,000 pairs (in 21 colonies), representing about 60% of the world population of this species (Mitchell *et al.* 2004). The colonies are widely distributed, but the majority of the population occurs in a few of the colonies: St. Kilda (Eilean Siar), Bass Rock (Lothian), Ailsa Craig (Ayr), Grassholm (Pembrokeshire) and Little Skellig (Kerry). The Gannet is Amber listed (Eaton *et al.* 2009) in Britain and considered a species of European conservation concern (Burfield & van Bommel 2004), because of this concentration at relatively few sites.

Summary of recent estimates

Gannets were the subject of an intensive programme on the Bass Rock from the 1950s through the 1970s (Nelson 1978), though relatively few have been ringed there since. Since the 1980s there have been a large number ringed elsewhere (particularly Ailsa Craig, Hermaness and Great Saltee), although most (97%) are ringed as chicks. Despite this Wanless *et al.* (2006) were able to estimate pre-breeding and adult survival by incorporating time-dependence in survival rates.

Issues for estimating survival rates

Gannets are large birds and nest at relatively low densities, so live-resighting studies based around field-readable rings or colour ring combinations is feasible for this species, however, the sites where this would be practicable may be limited. Many of the Gannet colonies in Britain and Ireland are in remote locations on high, near vertical cliffs or stacks such and reaching and subsisting on these in order to conduct work is difficult. Site philopatry (both of adults and, to a lesser extent, young birds) is high, so mark-resighting studies at particular sites should yield robust survival rate estimates. Within sites there is also a high level of micro-site fidelity, so sampling only parts of the colony should not lead to excessive capture heterogeneity, though care will be needed to determine a 'representative' portion of the colony to be studied, as there will be a tendency to study the edges of the colony where densities are lower, even though these may represent younger or poorer quality individuals.

As with several other seabird species, Gannets are nearly all ringed as young in the nest. The gannet shows a considerable southward movement during the winter with birds ranging along the Atlantic seaboard as far as tropical West Africa (Senegal), and to Gulf of Mexico on American side. This southward movements is more marked in first year birds, with some immature birds even remaining in the winter quarters, where they are more likely to be drowned in fishing nets or shot, during the summer (Wernham *et al.* 2002), meaning reporting rates are likely to be age-specific, which creates difficulties for estimating age-specific survival rates (though see Wanless *et al.* 2006).

4.4.1.3 Cormorant

Introduction

The cormorant is one of our largest seabirds, and two distinct populations are found in Britain: the nominate race *P. c. carbo* is found largely around our coasts, and *P. c. sinensis* which is common in continental Europe, but which is increasing markedly in numbers, mostly in freshwater habitats. Here we focus primarily on the coastal *carbo* population. The species

is Amber listed because a large proportion of the population breed in relatively few sites, and Britain holds a large proportion of the European population in winter (Eaton *et al.* 2009). Cormorants nest in open coastal sites, mostly on top of stacks or flat islands, with considerable differences between seasons and within colonies in the timing of laying (Mitchell *et al.* 2004). Small colonies, in particular, can be quite ephemeral, so breeding in one year is not necessarily a good predictor of breeding in the next. Immature birds will often turn up late in the breeding season in their second year and may build a nest, however they rarely breed until their third year, and usually not until their fourth or fifth (Coulson & Brazendale 1968).

Summary of recent estimates

Wernham & Peach (1999) analysed ring recovery data to assess changes in the survival of cormorants through the period 1965-94. As there were a large number of recoveries, they were able to estimate adult survival rates well but, because most birds are ringed as nestlings, they were unable to estimate juvenile survival without making restrictive assumptions about age-specific variation in reporting rates. There are a number of colour-marking programmes in operation on Cormorants, both in Britain and elsewhere western Europe (e.g. Fredeiksen & Bregnballe 2000). These tend to be focussed on particular colonies, which allows variation in survival rate between colonies to be accounted for using multi-state mark-recapture models (e.g. Henaux *et al.* 2007). Combining the mark-recapture with the recovery data has the potential to overcome the problems inherent in both datasets and provide annual survival rates with reasonable precision. There would also be potential for developing population models in this species which integrate survival, productivity and census data.

Issues for estimating survival rates

Ringing returns suggest that cormorant dispersal outside the breeding season is coastal rather than radial, with birds avoiding long sea crossings because of their need to roost on land. Although Stuart (1948) reports that movements which occur in the first winter are greater than those which occur in subsequent winters, Coulson & Brazendale (1968) found no such difference in movement with age. A large number of cormorant recoveries originate from birds that are shot as they are seen as a pest species competing for fish stocks. Both Newson (2000) and G. Smith *et al.* (2008) have produced models of Cormorant population dynamics, incorporating both coastal and inland populations, aimed at investigating the spread of colonies and the impact of control measures due to increasing conflict with the angling community.

4.4.1.4 Shag

Introduction

Shags are smaller than cormorants and are almost exclusively marine, being found mainly in coastal waters and sometimes estuaries. The shag is confined to the north-eastern Atlantic and Mediterranean, and Britain holds around 40% of the world population (Mitchell *et al.* 2004). Because of this (and the fact that most birds breed in a relatively small number of sites) the species is Amber-listed (Eaton *et al.* 2009). Shags can be found breeding in large colonies, in small, scattered groups or singly, with nest sites situated on exposed ledges or among boulders on cliff slopes and is highly influenced by environmental conditions, with large fluctuations in the date of return to the colony (between February and April) and breeding success between years (Snow 1960). Immature birds may breed at two years old but are more commonly older on their first attempt (3 or 4 years old), with young males tending to recruit earlier than females (Potts 1969, Aebischer 1986).

Summary of recent estimates

Four to five thousand Shags are ringed each year, although most (c 95%) are ringed as chicks. Additionally, there have been long-term colour-marking programmes at two of the larger colonies (Isle of May and the Farne Islands). Survival rates for both of these colonies have been estimated using combined mark-recapture and mark-recovery estimates to provide more robust estimates (Harris *et al.* 1994*a,b*; Catchpole *et al.* 1998; King & Brooks 2002). Both Harris *et al.* and Catchpole *et al.* estimated survival to breeding age and adult survival, while Catchpole *et al.* were further able to estimate separate survival rates for first year and second/third year birds. Survival of young birds is always lower than adult birds and Daunt *et al.* (2007) showed that, at least for first-year birds, this was related to reduced foraging efficiency.

Issues for estimating survival rates

Unusually for a seabird, Shags have a relatively 'wettable' plumage, which means they cannot spend extended periods at sea and so tend to remain fairly close to their breeding colony for much of the year. Recoveries also show marked differences between regions in the timing and extent of dispersal from colonies outside the breeding season, with a tendency for greater dispersal in populations on exposed coasts (Galbraith *et al.* 1986). As a result it is difficult to get representative data from one area only. Shag philoptary is high (at least in the colonies studied), with >90% of young and 99% of adult birds returning to breed at the same colony (Potts 1969; Aebischer 1995).

However, Shag reproduction and survival can show very large fluctuations between years and it is essential that any study of survival takes this into account. Years of fairly constant population parameters are interspersed with 'crash' years, when a large number of experienced shags do not breed (10-60%, Aebischer 1986, Harris *et al.* 1994*a*), or when large numbers of adults die in winter 'wrecks' (e.g. Harris & Wanless 1996). Low productivity is usually combined with 'eruptive' winter dispersal, where individuals move a much larger than average distance and a larger percentage of individuals move beyond their normal winter range (Potts 1969). Such eruptions are associated with high mortality, especially among first year birds (Harris *et al.* (1994*a*) recorded a first year survival of 56% in normal years, down to 17% in crash years). Crash years are reasonably common with Potts (1969) recording eruptive movements in 9 of 15 (60%) years 1952-65 on the Farne Islands, and Aebischer and Wanless (1992) recording widespread adult non-breeding in at least 3 (possibly 5) of the 15 years of continuous nest counts on the Isle of May. One needs to model such annual events in order to produce unbiased estimates of demographic parameters, which of course requires sufficient data (e.g. recoveries for estimating survival rates) although given the ringing effort for Shag these are probably available.

4.4.1.5 Kittiwake

Introduction

The Kittiwake is the smallest and most oceanic of our gulls, nesting mostly on sea-cliff ledges. The Kittiwake has a circumpolar distribution, consequently Britain and Ireland hold a relatively small fraction of the world population (<10%). As with many seabirds, because a large proportion of the population breeds at relatively few sites in Britain (mostly in Scotland) the species is Amber listed (Eaton *et al.* 2009).

Summary of recent estimates

Kittiwakes have been colour-ringed at a number of colonies, notably North Shields (Tyne & Wear) since 1949 (e.g. Coulson & Thomas 1985), but also Fair Isle (Rothery *et al.* 2002),

Foula (Oro & Furness 2002), Isle of May and Skomer. Shorter-term studies have also been conducted at a number of other colonies. Survival of Kittiwakes in the UK was first estimated by Aebischer & Coulson (1990) using a linear modelling approach and showed significant annual variation in return rates, as well as differences between breeding and pre-breeding birds and between adults which in the centre and edges of the colony. Elsewhere Danchin & Monnat (1992) and Hatch *et al.* (1993) used mark-recapture modelling to estimate adult survival rates in Brittany and Alaska respectively, while Cam *et al.* (2004) explored some of the ecological drivers of local survival patterns using a multi-state model in the Brittany colony. Sandvik *et al.* (2005) showed that survival of Kittiwakes in Hornøya (Norway) were related to climatic factors, particularly sea surface temperature. As with many seabirds, kittiwake population dynamics depend heavily on the availability of sandeels, but sea temperature (Frederiken *et al.* 2004a) and great skua predation (Oro & Furness 2002) have also been shown to influence survival rates. More recently, Frederiksen *et al.* (2004*b*) used Kittiwakes as an example to show how the use of individual covariates to model age-dependence, even though only adults may be ringed (perhaps not the most usual situation for a seabird study!) and Link *et al.* (2002) used a Kittiwake dataset to demonstrate how Bayesian techniques could be used to model individual heterogeneity in survival.

Issues for estimating survival rates

Although adults are likely to be site faithful in stable colonies, there can be significant interchange of both adult and juvenile birds between colonies (e.g. Coulson & Mévergnies 1992). The incidence of non-breeding by adults also seems to vary between colonies, with Wooller & Coulson (1977) and Richardson (1985) reporting significant numbers of missed breeding attempts, particularly by younger birds. However, Porter & Coulson (1987) found instances of non-breeding to be rare at their colony (North Shields) and Cam *et al.* (1998) found no evidence of an effect of breeding state on the probability of recapture.

Frederiksen *et al.* (2005) analysed patterns of breeding success at 42 colonies in Britain and showed strong regional variation in productivity in relation to variation in sandeel recruitment and it is likely that there will be similar regional variation in survival rates.

The only analysis of dead recoveries was by Coulson & White (1959); since then a reasonable number of Kittiwakes have been ringed each year (c.2,200), and of these a good proportion (c. 25%) are adults, though the proportion recovered (c. 1.5%) is low, as with most seabirds. As in many other seabird species, young kittiwakes tend to range further than adult birds (the coasts of Greenland and France being within the normal range of immature British-born kittiwakes), with the distribution of young birds becoming progressively more similar to that of adults up to the age of first breeding (Coulson & Mévergnies 1992; Wernham *et al.* 2002).

4.4.2 Burrow-nesting petrels

4.4.2.1 Manx Shearwater

Introduction

Although their breeding range stretches from Newfoundland, Canada through north-west Europe to the Azores, most (c. 90%) of the world population of Manx Shearwaters breed in Britain and Ireland, primarily in colonies along the west coast of each island. Because of this concentration in numbers, at relatively few colonies, they are Amber listed (Gregory *et al.* 2002), and similarly is regarded as a species of conservation concern in Europe (Burfield & van Bommel 2004).

Summary of recent estimates

The distribution within Britain and Ireland is extremely limited, with most birds nesting on the islands of Skomer, Skokholm (Pembrokeshire) and Rum (Inner Hebrides). The islands off St. Kilda, Bardsey, County Kerry and Lundy also have important breeding populations. As with other shearwaters, Manx Shearwaters are nocturnal making study of their populations more difficult. However, long-running ringing programs operate on Skomer, Skokholm, Bardsey (Gwynedd) and Copeland (Co. Down). There is also ongoing ringing of Manx Shearwaters on Sanda (Kintyre) which is registered as a RAS project. There appear to be no recent estimates of Manx Shearwater survival in Britain, or elsewhere, though analyses of the data from Skomer and Copeland are in preparation (the former were previously analysed by Perrins *et al.* (1973)).

A total of 320,000 Manx Shearwaters have been ringed (currently c. 4-5,000 annually), but the recovery rate is low (1.3%), although not unusually so for a seabird, and likely to be particularly heterogeneous given the wide non-breeding range.

Issues for estimating survival rates

The Manx shearwater is more difficult to study than most other seabirds as it is nocturnal and nests in burrows. This makes re-sighting colour rings impossible so recapturing birds, either at the surface or in their burrows, is the only means of obtaining survival rates from live CJS studies. Birds caught out of the burrows will include some non-breeders, though there is little information on the likely proportion, which will introduce problems of trap-dependence in the analyses and potentially lead to underestimation of survival rates. There are, however, methods are available to assess the strength of this problem, and control for it to some extent. This problem may be circumvented by ringing and recapturing birds prior to laying as these birds are most likely to be breeders with a very low emigration probability. Catching birds in burrows requires construction of inspection hatches in nesting chambers and may result in emigration due to disturbance. Breeding birds largely remain at the colonies to which they recruited (Perrins *et al.* 1973), though those moving to non-study burrows may be hard to detect; natal philopatry is apparently lower for females than for males (49% and 85% respectively, though sample sizes were not large; Brooke 1978).

Manx shearwaters can be captured easily on the surface of the colony at night, and large numbers have been ringed in this manner. However, most are pre-breeding birds that are prospecting different colonies, as adult breeding birds spend very little time on the surface (Harris 1966), so are unavailable to capture, hence capture rates are age-dependent. The problem with this approach is that recapture rates will be extremely low owing to the birds spending very little time at the surface. The recapture rate for this method is around 10% (Perrins *et al.* 1973), so it is likely that in the region of 300-500 birds would need to be ringed in each colony each year.

Both breeding and newly fledged Manx Shearwaters, disperse quickly in September, heading straight to South American wintering grounds off the coasts of Brazil and Uruguay (Wernham *et al.* 2002). However, younger birds remain at sea for the first few years of life, where they may be more at risk from the activities of French and Spanish fishing boats and are unlikely to be recovered dead at the breeding colony. This will create age-specific variation in the likelihood of a dead bird being reported. However, many Manx Shearwaters have been ringed as adults as well as chicks, so age-specific reporting rates may be estimable.

4.4.2.2 European & Leach's Storm-petrel

Introduction

Both species of storm-petrel that breed in Britain and Ireland represent enormous logistical and technical challenges in studying their populations. Both are nocturnal, breed in burrows or other cavities and colonies generally restricted to remoter (i.e. predator-free) islands off the west coasts of Scotland, Ireland and Wales. Indeed it was only during the Seabird 2000 survey that any sort of quantitative idea of their breeding location and numbers was obtained. Populations of both Leach's and European Storm-petrel are Amber listed in Britain (Eaton *et al.* 2009) and of conservation concern in Europe (Burfield & van Bommel 2004) because of a relatively high proportion of the world's population breeding there.

Summary of recent estimates

Storm-petrels are readily captured at their colonies and at headlands in mist nets in conjunction with playback of the male's purr call methods (Fowler & Hounsome 1998, Harris *et al.* 1998). It is one of the most commonly ringed seabird species in Britain and Ireland, but most birds are caught later in the breeding season, so non-breeders are more likely to be caught and in contrast to other seabirds, most birds are ringed as adults rather than chicks. The recovery rate is high for a seabird due to live recaptures in mist nets, but dead recovery rates are low due to their pelagic habits and small size meaning few are found. Despite the high ringing effort and recovery rates the accurate estimation of adult survival rates is problematic given the relatively high (and unknown proportion of non-breeding birds present in samples). Owing to the small numbers of birds ringed as chicks, the estimation of immature survival rates is not possible with the current data.

Insley *et al.* (2002) investigated methods of estimating survival rates, in particular by catching birds without the use of tape-lures, which gave an estimate similar to that derived from national recovery data, indicating that it may be possible to generate useful data for this species. Estimates of Leach's petrel are provided by Furness (1984) from St Kilda and Butler *et al.* (1988) from a Canadian population, although the latter were from birds involved in a study of the effects of pollution. For both species only average estimates were calculated, collecting sufficient data to estimate annual rates is likely to be difficult.

Issues for estimating survival rates

The breeding sites of Storm-petrels are very cryptic, usually being in cavities among boulders in beaches or scree or walls (Ratcliffe *et al.* 1996). Nest sites are therefore very difficult to locate and access for inspection. As a consequence, very few Storm Petrels have been ringed as chicks, making pre-breeding survival impossible to assess. Marking adults and recapturing or resighting them in the nest is also difficult and may cause problems of disturbance and desertion (Bolton 1996). The birds are exclusively nocturnal at the colony and during this time spend little time on the ground, either remaining aloft (especially non-breeders) or flying straight to the burrow (Scott 1970). This makes re-sighting studies of the type seabirds generally lend themselves to impossible and may bias captures towards the more aerial non-breeders.

Adults of both species tend to return to the same colony, often to the same burrow, though chicks are less likely to return to breed at the colony at which they were hatched. The probability of a bird being captured and recaptured in a mist net depends strongly on its breeding status. Breeders commute directly between their nest sites and the sea, whereas non-breeders circle the colony for prolonged periods and are therefore more likely to be captured and recaptured within a year (Love 1978). This problem is most acute for mark-recapture estimates of population size in which the ratio of marked to unmarked birds in catches is

important. With survival studies, the recapture history of birds in the years subsequent to recapture forms the focus of the analysis, and the main bias created by non-breeders in these analyses results from their low site fidelity. Heterogeneity can also arise among breeding birds due to breeders having a higher likelihood of being caught close to their nest site than further away. Storm Petrels tend to return to the same nest site or patch of nesting habitat year after year (Davis 1957, Scott 1970). In large colonies with discrete habitat patches (e.g. on a large island or on small islets in close-knit archipelago) mist netting at a single habitat patch will tend to result in birds breeding there being caught more than others, creating a trap dependence response and an under-estimation of survival rate. To circumvent this problem, birds should ideally be captured at a range of habitat patches within the colony, though the logistics of such an exercise on large islands or archipelagos may be formidable.

Intermittent breeding by experienced adults could also create heterogeneity in recapture rates in studies based on study burrows, and in recapture studies using mist netting if these birds do not return to the colony. Only 48% of burrow owners were known to be breeding in 1954, and 52% in 1955 (Davis 1957). In a Basque population of European Storm-petrels, Hémery *et al.* (1986) reported that about 31% of mature adults did not breed in successive years. If certain birds tended to take consecutive years off breeding more than others, this would create trap dependence and underestimate survival rates in a similar manner to above.

4.4.3   Skuas and Gulls

4.4.3.1   Arctic Skua

Introduction

Although the Arctic Skua has a circumpolar range, in Britain it is found mostly on the northern and western isles, with a few scattered mainland colonies, a range that has remained largely unchanged for at least the last 150 years (Mitchell *et al.* 2004). Although the population overall has apparently declined in recent years, rates of population change do vary between colonies, with some increasing markedly whilst others are decreasing. Despite the apparent moderate decline overall the species is not listed of conservation concern (Gregory *et al.* 2002), although recently it was made the subject of a Biodiversity Action Plan.

Summary of recent estimates

Arctic Skuas have been the subject of long-term monitoring on both Fair Isle (O'Donald 1983) and Foula (Phillips & Furness 1998). Estimates of return rates of breeding birds from colour-ringed individuals were calculated for the Foula population by Phillips & Furness (1998). Unusually, the resighting rate was considered to be 100% in this study, so there was no need to correct for birds that were alive but missed. Such estimates will be lower than the true survival rate, to the extent that breeding birds emigrate to other colonies; given their high site fidelity (below) this bias may be low.

Issues for estimating survival rates

Arctic Skuas tend to nest at low densities, requiring extensive study areas to encompass an adequate sample size of birds. The resighting studies conducted so far on Fair Isle and Foula are discrete, high density colonies at which recruitment and survival may not be representative of those elsewhere. Adult Arctic Skuas can be hard to catch; however, colour-ringed individuals are relatively easy to resight in the breeding areas. Once they start to breed adults appear to be highly site faithful, though they will occasionally miss a breeding year, remaining at sea during the summer months (Furness 2002); estimates of the incidence of non-breeding vary between 0 and 12% (Phillips *et al.* 1996; Catry *et al.* 1998; Phillips &

Furness 1998). This implies that estimates of survival from mark resighting studies may be sufficient to get a reasonable idea of 'true' survival rates.

Recoveries in Shetland show that a substantial number of young birds do move between colonies, suggesting that natal philopatry is low. This means that more extensive effort (or mark-recovery studies) will be required to estimate immature survival rate. Outside the breeding season, Arctic Skuas can range widely, as far as South Africa and even South America. However, some individuals remain in northern waters, and some may even visit colonies in their early years, creating a high degree of heterogeneity in reporting rates and problems for analysing immature survival rates using mark-recovery methods.

4.4.3.2 Great Skua

Introduction

Scotland holds the majority of the world's population of Great Skuas (60%), which is confined to northernmost Europe (Mitchell *et al.* 2004). Numbers are increasing markedly throughout its range (both in Britain and elsewhere), but the species is Amber-listed in Britain (Eaton *et al.* 2009) because of the concentration in population numbers.

Summary of recent estimates

There has been a long-term of study of Great Skuas on Foula (the largest colony in the world), with colour-ringing and resighting also occurring for a number of years on Handa and St. Kilda and at Hermaness. Ratcliffe *et al.* (2002) analysed resighting records for colour-ringed breeding birds on Foula from 1988 to 1999. The best fit model allowed time dependency in both survival and resighting probability. Survival rates followed a trend, declining between 1989 to a low point in 1991, increased to a plateau between 1994 and 1996 before declining again in 1997. This appeared to be associated with changes in sandeel abundance in Shetland waters. They also found significant difference in survival with age.

Hundreds of Great Skuas on Foula have been trapped as non-breeders on club sites, a large proportion of which were ringed as chicks. These have the potential to produce estimates of survival from fledging to attendance at club sites using a recruitment analysis (Pradel and Lebreton 1999). Captured birds were colour-ringed and these have been re-sighted on club sites and as recruiting birds, which could give estimates of survival between arrival at the clubs at ages 3-4 and recruitment into the breeding population at ages 5-8. The analysis will be complex, including resighting and recapture rates that are likely to be heterogeneous since the birds on the club sites near the fieldwork accommodation were trapped and re-sighted more intensively and birds show fidelity to individual sites (Klomp and Furness 1992*b*).

Issues for estimating survival rates

A high degree of micro-site natal philopatry is seen in great skuas, with young birds often recruiting onto breeding sites close to where they hatched within the natal colony (Klomp & Furness 1992*b*). However, the growth rate of the population at St. Kilda suggests that as many as half of the birds recruiting between 1994 and 1997 (Phillips *et al.* 1999a) were immigrants and those that could be linked to natal sites originated from Shetland, indicating a significant degree of natal dispersal. Breeding philopatry of adults is high and any movements within a colony are usually short (Catry & Furness 1997; Catry *et al.* 1998). However, a proportion of the population may not breed every year; Catry *et al.* (1998) recorded that 9% (range 4-14%) of experienced great skuas deferred breeding for at least one year, potentially creating heterogeneity between individuals in re-sighting rates. Ratcliffe *et al.* (2002) also report heterogeneity between individuals as a result of non-breeding and that great skuas were

particularly trap-shy for several years following initial capture, which is one of the benefits of colour-ringing, in that individuals do not need to be re-captured.

Encouragingly, Klomp & Furness (1992*a*) found that retention of colour-rings on great skuas was relatively high, with only two of 784 colour-rings placed on 196 breeding skuas (4 per bird) 1988-90 being lost, and none of 494 non-breeding birds were seen to lose any colour-rings at all during this time period. Ratcliffe *et al.* (2002), however, report that 5.6% of birds lost one or more colour rings during 9 years of study.

A large number of great skuas are ringed each year (c. 1,500), but most (99%) are ringed as chicks, meaning an analysis of survival rates using mark-recovery data alone is likely to be difficult due to large heterogeneity in reporting rates between age classes. This is compounded by different age classes of great skua showing marked variation in their marine ranges and mortality causes (Furness 1978, 2002). The winter movements of adults appear much less extensive than those of younger birds. Recoveries comprise 28.9% first year of life when the young birds are becoming independent. After fledging first year birds make a progressive southward movement along with the other age groups, mainly via the North Sea (Klomp & Furness 1992*b*). This movement occurs at a very variable rate, with some birds having covered 3000 km by the end of August, whilst others can remain around Shetland until December. They do not return northwards with the adult birds in April though (many are recovered shot in Iberia) and are largely pelagic through their first summer. In their second and third years the immature birds continue a largely pelagic existence, generating few recoveries. They do, however, show a summer tendency to return north to the breeding areas, and many 2 and 3 year old birds are found in Arctic regions where many are shot (Faroes and Greenland).

4.4.3.3 Black-headed Gull

Introduction

The Black-headed Gull is an adaptable species, and has become increasingly terrestrial over the last century or so (Holloway 1996), although its range may have been more extensive before large areas of wetland were drained in the 16th and 17th centuries. In fact now it can be considered almost as much a bird agricultural ecosystems as marine ones. Overall, numbers in both coastal and inland areas have shown little change in the recent years, though there is quite a bit of regional variation, for example Scottish coastal populations are decreasing, while numbers inland are increasing (Mitchell *et al.* 2004).

Summary of recent estimates

Although large numbers of Black-headed Gulls are ringed, both as chicks and adult birds, there do not appear to be any estimates of survival rates for British birds using modern methods. Estimates of survival rates have however, been calculated from resightings of colour marked birds in the Netherlands (Majoor *et al.* 2005) and France (Prevot-Juillard *et al.* 1998).

Issues for estimating survival rates

Analyses of survival rates in the French colony have been complicated by problems of trap-dependence (birds at the water's edge are easier to re-sight) and transience (birds not remaining resident in the colony), but analytica methods are being developed to model such subtleties in the data (e.g. program E-Surge, Choquet *et al.* 2008), though these require large amounts of data from each site to estimate all the required parameters effectively. Prevot-Julliard *et al.* (1998) reported little dispersal of adults from their breeding colony, but this was a large, stable colony where dispersal might be expected to be limited. The median distance ringed adults moved between breeding seasons in Britain was 29km, suggesting significant breeding dispersal (Wernham *et al.* 2002). Natal dispersal is higher, and birds in their first

year range widely, even as far as North Africa, creating a high degree of reporting heterogeneity.

As with other gulls a high proportion of birds are ringed in winter and away from breeding colonies, so are of little use in estimating survival rates (though they yield much information on patterns of movement).

4.4.3.4 Common Gull

Introduction

The Common Gull is a medium sized gull that breeds in both coastal and inland areas, primarily in Scotland and Ireland. The species is Amber listed (Gregory *et al.* 2002) based on a moderate population decline in the last 25 years and similar declines across north-west Europe mean that it is also a species of European conservation concern (Burfield & van Bommel 2004).

Summary of recent estimates

The only published information on Common Gull population dynamics is a comprehensive study on the ecology of the common gull was initiated in 1962 by Steve Onno, at a colony on three small islets in Matsalu Bay in western Estonia (e.g. Larsson *et al.* 1997). About 90% of the breeding adults are ringed (colour-ringed since 1971) and each year about 95% of the chicks are marked. Rattiste & Lilleleht (1987) present survival estimates derived from the return of colour-ringed birds to this colony for first year second/third year and adult birds.

About 90,000 Common Gulls have been ringed in Britain and Ireland, mostly as chicks. A reasonable number of adult birds have been caught (c. 12% of all ringings), but these will mostly have been caught at landfill sites in the winter months, when birds from Britain mix with others from north-east Europe, limiting their usefulness in calculating survival rates of the British population.

4.4.3.5 Lesser Black-backed & Herring Gulls

Introduction

The Lesser Black-backed Gull is essentially a European gull, breeding in northern Europe (and western Siberia) and wintering in south-western Europe and north Africa. About 40% of the world population breeds in Britain, and because of this it is Amber listed (Eaton *et al.* 2009), although overall populations are increasing markedly. The closely related Herring Gull is often found breeding in the same colonies (where the ranges overlap) and has very similar breeding biology, though it tends to be less migratory in winter. It is Red listed both because the population is localised and because of a recent population declines (Eaton *et al.* 2009).

Summary of recent estimates

A mixed colony of Lesser Black-backed and Herring Gulls became established on Walney Island in Lancashire in the 1920s. Rapid explosion of the population occurred during the 1950s, perhaps as the birds learnt to exploit the local fisheries and rubbish tips for food and by the 1960s there was roughly 9000 breeding pairs of each species (Brown 1967). Although there has been much work done on reproductive success and chick survival at this colony (e.g. Monaghan *et al.* 1998, Kim & Monaghan 2005) there has, as yet, been no published analysis of survival rates.

Both Lesser Black-backed and Herring Gulls have been ringed on Skomer and Skokholm Islands since 1968, and a number of papers relate to the results obtained. Todd (1987) presents estimates for adult survival in herring and lesser black-backed gulls from 1978, and these are updated in Poole *et al.* (1998). The survival rate of Lesser Black-backed Gulls was found to have declined gradually through the study (97.6% in 1978, to 80.6% in 1994), and the survival rate of herring gulls on Skomer has been quite variable. Harris (1970) estimated first year survival in herring gulls from metal ring recoveries, but had to make a number of restrictive assumptions about survival rates of immature birds. More modern analytical methods should mean less restrictive assumptions are required, and so better estimates of survival rates should be possible.

Colour-ringing of both adult and young herring gulls has been carried out on the population on the Isle of May since 1968. The Nature Conservancy Council began culling these birds in 1972. Between 1989 and 1993, breeding Herring Gulls and Lesser-black-backed Gulls have been trapped and colour-ringed to maintain marked populations of around 150 birds for each species. Resightings of these birds up to 1993 were analysed and no time dependence or differences between sexes in survival rates were found over this period (Wanless *et al.* 1996). Chabrzyk & Coulson (1976) analyse metal ring recoveries from chicks ringed on the Isle of May to estimate the survival of young herring gulls to breeding age. In this calculation, like Brown (1967) and Harris (1970), they assume that all of the differential survival takes place in the first year of life and that survival rate of immature birds after their first year is thus the same as the adults. Coulson (1991) updated this estimate, allowing for an emigration rate of 70%.

A large number of these species are also ringed as part of ongoing volunteer-based studies in the Severn basin; these data have yet to be analysed systematically but would provide a valuable opportunity for looking at patterns of survival and movement.

Issues for estimating survival rates

Once they have bred, the large gulls show strong site-tenacity, with any movement of sites usually associated with heavy disturbance (e.g. Tinbergen 1953). Of 55 breeding adult herring gulls ringed and recovered on the Isle of May (with an average of 5 years between records), 84% were found in same sub-colony, and 11% in adjacent areas (Chabrzyk & Coulson 1976). This suggests that colour-mark studies could yield useful estimates of adult survival rates for monitoring purposes. Coulson (1991) estimated that there was some degree of natal philopatry on the Farne Islands, with 55% of Herring Gulls and 53% of Lesser Black-backed Gulls returning to breed on their specific island of birth. He also estimated that on the Isle of May rates of 30% philopatry were not unreasonable for herring gulls, which agrees with the conclusion in Chabrzyk and Coulson (1976), though this varies significantly between the sexes (with males more likely to be found breeding in their natal area.

Estimates of non-breeding in Herring Gulls range from 15-30% (Kadlec & Drury 1968) up to as many as 50% of birds of 4 years and older (Migot 1992). Calladine & Harris (1997) recorded that c. 35% of adult Herring Gulls and Lesser Black-backed Gulls, all with some previous breeding experience, failed to breed in a two year study. As has been found in a number of other studies (*e.g.* Harris & Wanless 1995), non-breeding did not occur at random at the individual level, with about half of the known intermittent breeders failing to breed in both years of the study. Such high levels of non-breeding will introduce capture heterogeneity into the data, which will need to be accounted for in the analyses and which may reduce the precision of any estimates of survival rates obtained.

Both species disperse away from the breeding grounds in the winter months. Herring gulls tend to disperse predominantly in a southerly direction, but the majority remain to winter within the British Isles, with very few reaching the continent (Wernham *et al.* 2002). Kilpi &

Saurola (1983) found that adult and juvenile gulls tended to use the same wintering areas, with apparent 'local dispersion zones' for separate colonies. Lesser Black-backed Gulls migrate much further than Herring Gulls, with wintering birds spreading southward through Spain and the Mediterranean, down as far as equatorial Africa (Wernham *et al.* 2002); however, an increasing number of birds are wintering in northern Europe.

This wide wintering area will create a great deal of heterogeneity in the reporting rates of both dead birds and, increasingly, colour-marked birds. However, both species winter largely in European coastal areas, so problems of reporting bias will be less than for many species of seabird.

Since the 1970s all large gull species have been artificially controlled to some extent; many metal ring recoveries for large gulls are obtained from these culls, and it is important to consider their effect on adult emigration, natal recruitment and breeding density (and therefore density dependent effects such as age of first breeding, egg size, breeding success, Coulson 1991).

4.4.3.6 Greater Black-backed Gull

Introduction

Great Black-backed Gulls are the largest and most marine of the *Larus* gulls breeding in the UK, though probably also the least studied as it tends to nest on sparsely populated islands and other locations that are difficult to access (Mitchell *et al.* 2004). This has implications for survival estimation, as few colonies have sufficient birds to allow marking of an adequate sample of birds for CMR estimation and, as with other seabirds, the demography in big and small colonies could be quite different. Overall numbers have remained largely unchanged in the last twenty years and the species is not of conservation concern.

Summary of recent estimates

There appear to be no recent estimates of survival rates in Greater Black-backed Gulls, perhaps because relatively few are ringed each year (c. 2,200) virtually all (>99%) as chicks. Greater Black-backed Gulls are less migratory than either of the other large gulls, so heterogeneity in reporting rates should be less, though there may be a greater degree of age-related variation (as it takes longer to reach breeding age).

4.4.4 Terns

Terns share very similar patterns of nesting biology, life-history and dispersal, so the issues relating to survival rate estimation are similar for all five species that regularly breed in Britain. Consequently, we review recent survival rate estimates for each species first, and discuss issues relating to mark-recapture and ring-recovery for all species towards the end.

4.4.4.1 Sandwich Tern

Introduction

The Sandwich tern is the largest of the five species of terns which breed in Britain and Ireland. They nest in almost all coastal European countries from the Baltic and North Sea, and down the Atlantic coast through the Mediterranean. They also nest on the other side of the Atlantic from north east USA down to Argentina. Roughly 15,000 pairs breed in Britain and Ireland, or about 15% of the European population (Mitchell *et al.* 2004); this represents a decline in numbers of c. 10% since the previous seabird census in 1988-91. The Sandwich tern is Amber listed because a large proportion of birds breed at relatively few sites (Eaton *et*

al. 2009); it is also listed as of conservation concern in Europe, because of a moderate population decline (Burfield & van Bommel 2004).

Summary of recent estimates

Green *et al.* (1990) estimated survival of adult and juvenile (to breeding age) of terns using dead recoveries. They only used data from 1966 onwards, and only for birds up to 11 years of age, in order to avoid excessive problems with ring loss. They were able to overcome the problem of birds mainly being ringed as young to some extent by augmenting the ring recovery data with counts of breeding pairs and estimates of productivity from 60% of British colonies. This allowed time and age specific estimates of survival rates without assuming a constant reporting rate. By calculating the cohort recovery rates for 0-1, 1-3 and 3-11 years, as proportions recovered in each time period, and incorporating population size and average productivity into the model, Green *et al.* (1990) were also able to estimate survival to breeding age. More recently, Robinson *et al.* (unpubl.) were also able to estimate age-specific survival rates for the period 1990 to 2006, but were unable estimate survival rates on an annual basis due to lack of data.

4.4.4.2 Roseate Tern

Introduction

The roseate tern is one of the rarest breeding seabirds in Britain and Ireland, with a population of around 800 pairs (of which 740 occur in just two colonies in Ireland, Rockabill, Co. Dublin and Lady's Island Lake, Co. Wexford). It is Red listed as a result of a rapid population decline in Britain (Eaton *et al.* 2009), though numbers in Ireland are increasing (Mitchell *et al.* 2004). It is also of conservation concern at a European scale as a result of a relatively small population size (Burfield & van Bommel 2004) and is also listed on Annex 1 of the EC Birds Directive 1979.

Roseate terns usually nest in close association with other terns such as common and Arctic, but they often breed with less synchrony and their nest sites may be relatively well concealed (e.g. down burrows). Young adults usually arrive back at the breeding colony in their first or more commonly second summer, though they do not usually breed in their first year of colony attendance (Green 1995, Ratcliffe 1997, Ratcliffe *et al.* 1998).

Summary of recent estimates

Because of their conservation interest, there has been much interest in roseate terns, with a long-term colour marking programme operating, with Green (1995) and more recently (Ratcliffe *et al.* 2008) producing survival rates from this data. Green (1995) encountered a number of problems in fitting a standard CJS model to the data from Rockabill because birds showed a tendency to be re-sighted in the sub-colony where they were previously seen or ringed, and sub-colony coverage changed markedly through the study. Also it was easier to read rings in some areas of the sub-colony compared to others. More recently, Ratcliffe *et al.* (2008) estimated survival at three primary breeding colonies and again found problems with transience and trap-dependence in the data, but they were able to model these using a multi-state approach with time-dependent individual covariates.

Green (1995) also analysed the metal ringing recoveries of roseate terns ringed in Britain and Ireland between 1949 and 1992. The data were truncated to allow estimation of survival for birds aged 2-10 years only, as recovery rates were relatively constant through this period. An analysis was attempted to construct a joint model of both the re-sighting and the recovery data to estimate survival and movement rates between colonies, but this proved difficult due to the lack of recoveries during the period when re-sighting data were available (N. Ratcliffe pers.

comm.). Elsewhere, Spendelow *et al.* (1995) estimated annual adult survival rates from four of the largest colonies in the north-eastern US, which showed that time and location specific survival, movement and recapture probabilities were required to model this meta-population.

The roseate tern population currently effectively consists of two sub-populations, on the English east coast and in the Irish Sea, with very contrasting fortunes, consequently, the demography of the two populations is likely to be different, and should be modelled separately, although survival between the two areas is likely to be similar (all birds winter off the coast of west Africa). Although adults often return to the same colony, or even sub-colony (Spendelow *et al.* 1995; Green 1995), Ratcliffe *et al.* (2008) did note some movement between colonies, with breeding dispersal being highest towards the largest (and most productive) colony.

4.4.4.3 Common Tern

Introduction

Common terns nest throughout temperate Europe and Asia, from Arctic Asia down to West Africa and the Middle East. Although numbers are declining in Britain (especially Scotland), numbers in Ireland are increasing; the species is not of conservation concern in Britain. Common Terns nest in dense colonies of usually fewer than a 1000 pairs on low-lying coastal islands and shingle beaches, though as much as 10% of birds may breed inland, for example at gravel pits. Birds arrive at the breeding colonies in April and while young birds sometimes return and attempt to breed at the natal colony in their third year, but they are rarely successful and recruitment occurs more commonly at age 4 or 5 (Nisbet 1978).

Summary of recent estimates

There appear to be few recent published estimates of survival, although Nisbet & Cam (2002) estimated survival rates for a subset of birds of known age in a colony of birds in the USA (see also Nisbet 1978) and DiCostanzo (1980) estimated adult survival for birds at Great Gull Island (New York) using both time-specific and dynamic life-tables. Ezard *et al.* (2006) looked at the contribution of survival and reproduction in relation to population change in a German colony and found that return rates of juveniles were important in driving changes in numbers of birds.

4.4.4.4 Arctic Tern

Introduction

The Arctic tern has a circumpolar breeding distribution in the northern hemisphere, with the largest breeding populations in Arctic Russia, Canada, Alaska, Greenland and Iceland; British and Irish colonies represent some of the species' most southerly breeding sites (Mitchell *et al.* 2004). Most Arctic tern colonies have undergone a substantial decline in numbers in the last two to three decades, and overall there was a 29% decline between the mid 1980s and 2000; this is sufficient for the bird to be Amber listed as a species of conservation concern (Eaton *et al.* 2009).

Arctic terns often form large and relatively dense colonies on a wide variety of nesting habitats both inland and on the coast, including grassland, dunes, moorland and offshore islands. Arctic terns tend to migrate earlier and farther south than common terns spending the winter in the southern hemisphere, with some birds showing transatlantic migration and wintering off south American coasts (Wernham *et al.* 2002). In the first few years after fledging young birds remain in the wintering grounds and though many three year old birds

return to colony, most do not breed until their fourth or possibly fifth year of age (Cullen 1957, Coulson & Horobin 1976).

Summary of recent estimates

There has been a long-term ringing programme of Arctic terns on the Farne Islands, which began as early as the 1930s; more recently a significant number of birds have been colour-ringed. Coulson & Horobin (1976) captured and resighted birds on the Farne Islands from 1966-68 to obtain an estimate of adult survival from the proportion of birds alive in one breeding season and identified the next. They also estimated adult survival from the return of marked birds, plotting the log of the numbers of birds seen by age and fitting a slope by the method of least squares (as done by Austin & Austin (1956) for common terns). However, this is likely to be an under-estimate since they assumed that the breeding population was closed. They also present an estimate of survival through the first year of life, based on the assumption that after this first year (by which time most young terns will have mastered the necessary fishing skills) and suggested that the survival rate of immature terns was roughly equal to that of adults.

4.4.4.5 Little Tern

Introduction

The smallest of the terns breeding in Britain and Ireland, the little tern has a wide breeding distribution in Europe, Asia and Africa, with Britain and Ireland hosting about 10% of the European population (Mitchell *et al.* 2004). Like all the other terns, the little tern is listed on Annex 1 of EC Birds Directive (EC/79/409). It is also of medium conservation concern (Amber) in Britain because of a moderate recent population decline and localised breeding population (Eaton *et al.* 2009). Similar declines across Europe have lead to it being considered of conservation concern at that scale too (Burfield & van Bommel 2004). Perhaps because it breeds in relatively small, and often accessible, numbers and productivity have been comprehensively monitored on an annual basis (Sears & Avery 1993).

Most colonies are small, with usually less than 20 pairs nesting in a small group on sand, gravel or shingle beaches or islands. Information about little tern movements is relatively sparse, though it is likely that they winter in near-shore waters in West Africa (Wernham *et al.* 2002). Young birds do not usually return to the colony in their first few years of life, with first breeding usually occurring at three years of age (Massey *et al.* 1992).

Summary of recent estimates

Grosskopf (1964) estimated adult survival to be 80% from German metal ring recoveries of little terns. However, Sears & Avery (1993) suggested that results such as this from outside Britain may not be applicable, since British and Irish colonies may form a closed and self-sustaining population.

Issues of survival rate estimation in terns

Terns can be very erratic in their choice of nesting sites and they are prone to disturbance by humans or mammalian predators and whole colonies may desert and fail. Extra caution thus needs to be exercised when ringing birds at the breeding colony (as virtually all terns are) to avoid disturbance, ringing at tern colonies is often restricted and this may limit the numbers that can be practically ringed. Similarly, terns have a tendency to occupy colonies rapidly and synchronously with relatively low site tenacity (Evans 1982). These characteristics make it difficult for long term study of the terns at single breeding colonies, and mean that a wider meta-population approach is often needed. In order to gain accurate estimates of survival, this

movement between colonies will need to be taken into account by using recently developed multi-state mark-recapture models (Williams *et al.* 2002), as has been done recently for roseate terns (Ratcliffe *et al.* 2008). Such models require large numbers of birds to be colour-marked every year in order to estimate the required survival and dispersal parameters with sufficient precision. This is likely to work best for species with relatively few large colonies, such as Roseate and Sandwich Tern. For other species there are so many sites that vary greatly in size it would not be possible to estimate true survival as some birds would always end up in colonies without re-sighting effort. It might be possible to model emigration using size of, and distance to, other colonies to produce a holistic estimate though.

After breeding, terns move southward to winter in offshore waters round Africa. Young birds remain in these southerly waters through their first few years and are thus subject to greater mortality, with the majority of winter returns of these birds being trapped, intentionally or unintentionally. In addition to this, birds of the different age classes occupy different parts of the winter range or migrate at different rates. These differences in range and experience of young and old birds are important, because most terns have been ringed as chicks (Wernham *et al.* 2002), so age-related reporting rates are difficult to separate from age-related survival (Green *et al.* 1990). A further problem, common to all terns that winter in African waters, particularly those that fish closer inshore, is potential ring loss due to removal by locals collecting 'trinkets' (Becker & Wendeln 1996). However, the extent of this problem, and the likelihood of survival of any birds so caught and released, is unquantified.

4.4.5   Auks

4.4.5.1 Guillemot

Introduction

The Guillemot is our most abundant breeding seabird, with a population estimated in the region of 1.5 million birds, which is approximately a third of the European total (Mitchell *et al.* 2004). Because of this, and the concentration of a large number of individuals at relative few sites, the Guillemot is Amber listed (Eaton *et al.* 2009).

Guillemots can nest at a higher density than any other bird, with an average density on broad flat rocky areas of about 20 pairs m^{-2} (Harris & Birkhead 1985). They breed in crowded colonies on offshore islands, rock stacks and steep mainland cliff ledges. Breeding birds show a longer period of colony attendance prior to egg-laying than many other seabirds, with some individuals making their first brief visits to the colony immediately after the completion of primary wing moult in October (Harris & Wanless 1990). Once fledged, young birds do not start to visit the colony until their second year of life, congregating in clubs on the intertidal rocks. As they reach breeding age they spend progressively longer at the breeding colony and begin to arrive progressively earlier, moving up onto the breeding ledges away from club sites (Harris *et al.* 1986, Halley *et al.* 1995).

First breeding has been recorded at as young as 3 years at an expanding population on Canna (Swann & Ramsay 1983), but recruitment to the breeding population occurs more commonly at 5 or 6 years of age (Isle of May, Halley & Harris 1993, Harris *et al.* 1994*c*; Skomer, Birkhead & Hudson 1977).

Summary of recent estimates

The Guillemot has been the subject of intensive studies at a small number of colonies around Britain, consequently annual patterns of survival are relatively well-known. The population on the Isle of May went through a period of rapid increase, so that from 1969-85 the population roughly doubled in size (Harris 1991). Numbers then stabilised in the mid-1980s,

and the population began to decline by an average of 1% per annum (1983-94, Harris *et al.* 1996*a*). Survival rate estimates from the Isle of May all fall within this later period of stabilisation and slight decline. Adult birds have been colour-ringed and their subsequent return studied since 1981, pulli have also been given year-specific colour-rings at fledging since 1983. A number of papers refer to the findings from these data (*e.g.* Harris & Bailey 1992, Harris *et al.* 1992, Harris & Wanless 1995, 1996, Harris *et al.* 1996*a*, 2000, 2007) and show clearly the link between food resources and survival. The estimates have included both adult and juvenile survival and combine re-sighting and recovery data. Harris *et al.* (2000) also included colonies on Canna and Colonsay on the Scottish west coast in their estimation of survival rates, and there was some evidence of inter-colony differences in survival rates. More recently, Reynolds *et al.* (2008) reanalysed the data from the Isle of May in the context of an integrated population model and were able to derive more robust annual survival rates of both adult and juvenile birds as a consequence.

Population studies on Skomer, involving colour-ringed individuals, have been conducted since the early 1970s, when the population was at a low point, and have charted a marked rise in colony size (Hudson 1985; Hatchwell & Birkhead 1991, Poole *et al.* 1998). Again survival rates for adults and immatures have, in the main part, been calculated as simple return rates. Breeding birds were mainly captured on narrow ledges to reduce problems with ring loss, and unlike on the Isle of May, studies on Skomer recorded an increased tendency to move breeding site in the year after capture, so that data from this year were not included in analyses (Hatchwell & Birkhead 1991, Birkhead & Hudson 1977). Data from 1986 onwards have been modelled to estimate adult and pre-breeding survival rates in relation to environmental conditions, with survival being lower during years with higher sea-surface temperatures and in years with large oil spills (Votier *et al.* 2005, 2008).

Wernham *et al.* (1997) presented a comprehensive study of British and Irish metal ring recoveries for guillemots 1985-94. There have been 5734 recoveries of guillemot rings between 1918 and 1995, however only the 2728 of these recoveries that refer to birds ringed with the stronger incoloy 'guillemot specials' as introduced early 1980s to reduce problems with ring loss were used (also discarding 504 recoveries with inaccurate finding dates). Further restricting recoveries to only birds ringed in June and July kept the ringing period short compared to the recovery period, and leaves the 1575 recoveries from birds ringed as nestlings and the 98 recoveries from birds ringed as adults used in this study. This illustrates one of the problems with using ring-recovery data – apparently large sample sizes can dwindle quite quickly! They were able to differentiate four age-classes (first, second, third, and four year and older). Survival rates were dependent on year, though reporting rates were not and young birds (1-3 yrs, 3.4%) had higher reporting rates than adults (1.3%).

Issues for estimating survival rates

The representativeness of the study colony, and plots within a study colony, is an important consideration for studies on Guillemots. There is some evidence of differences in survival rates between colonies (Harris *et al.* 2000) but, on the Isle of May at least, no differences in survival rates of breeding birds at five sites within a colony of about 1300 pairs, despite these having differing cliff types and breeding densities (Harris & Wanless 1995).

Calculations suggest that as many as 42% of surviving young may emigrate, recruiting into breeding colonies other than the one in which they were raised (Harris *et al.* 1996*a*); as a result estimates of juvenile survival from the return rate of colour-marked young are likely to be underestimated. Of those birds that do recruit into their native colony however, micro-philopatry seems quite high, ranging from 79% of birds recruiting to their native sub-colony (Canna, Swann & Ramsay 1983), through to 42% (Isle of May 1983-94, Harris *et al.* 1996*a*), although the two estimates are not directly comparable since the size of the groups differed. Movement within the colony can create large variation in the reporting rate, particularly if

studies focus on a particular area within the colony. Once they have bred, as in many other seabirds, adult guillemots appear highly site faithful with estimates of site tenacity in adults that return and breed ranging from 96% (Aberdeenshire, Southern *et al.* 1965; Skomer, Birkhead & Hudson 1977) and 99.3% per year (Canna, Swann & Ramsay 1983), to 91% per year (Isle of May 1982-93, Harris *et al.* 1996*b*). This suggests that return rates may be a good proxy for survival rates for birds of breeding age, but that estimates of immature survival need to be derived from mark-recovery data.

In general, breeding Guillemots are intolerant of disturbance, with Hatchwell & Birkhead (1991) finding problems with birds moving site or showing reduced survival after trapping and Wernham *et al.* (1997) finding that survival and reporting rate differed between the first year after ringing and subsequent years. However, no adverse effects of ringing were found on the Isle of May (Harris & Wanless 1995, Harris *et al.* 1996*b*). The inaccessibility of the steep cliff ledges which Guillemots favour for breeding makes marking studies difficult and many colonies can only be approached from the water in boats; suitable catching and subsequent re-sighting areas can also be hard to find. (e.g. Harris *et al.* 1992, Halley & Harris 1993). Consequently, care will be needed if sites to monitor survival rates are to be established, but the existence of some sites already suggests that this should be possible.

Because of their habit of shuffling around on rocky cliff-ledges, ring wear (and loss) is a greater issue in Guillemots than in many other species. Special metal rings with stronger incoloy were introduced for Guillemots in 1983. These rings are shaped to fit the tarsus (triangular) and present the ring number upright on both sides of the leg. Wear on the inscription in these 'Guillemot specials' is greatly reduced compared with the previous wrap-around style of ring (Halley & Harris 1993). Wernham *et al.* (1997) suggest that without an estimate for ring loss (that can be used as a correction in models) only more recent recoveries from rings fitted after 1985 can be reliably used.

Harris & Wanless (1995) reported extensively on adult non-breeding in the guillemot. They found that 5-10% of birds known to be alive in any year did not breed, with 35/95 (37%) birds followed for ten seasons not breeding in at least one year. However, non-breeding did not occur at random in the population, with 6% of birds (*n* = 496 birds), accounting for 47% of the cases of non-breeding. It appeared that non-breeding was socially induced, mostly occurring after an individual had lost its site, and on average non-breeders appeared to survive less well (87%) than breeders (95%), with their previous season's breeding success being substantially lower than average. Harris & Wanless (1995) record, however, that of the birds not breeding in a particular year, in only 9% of cases was the bird absent from the colony for the entire season. Thus, although non-breeding birds are less likely to be recaptured than breeders, the high incidence of adult non-breeding may not pose a large problem.

Return rates for metal rings placed on guillemots in Britain and Ireland are higher than for other seabirds (close to 3% of guillemot rings are recovered), which probably reflects the propensity for Guillemots to be affected in pollution incidents, particularly oil spills (Wernham *et al.* 2002). Also, the majority are ringed as young (c. 85%) and at the breeding colonies in June and July (99%). This causes problems with potential biases in reporting rate differences between juvenile and adult birds due to differences in their ranging behaviour and experience. Birds in their first year disperse further than older birds and are more vulnerable to being shot or drowned in fishing nets, perhaps through lack of experience.

4.4.5.2 Razorbill

Introduction
Like the Puffin, the Razorbill breeds only in the North Atlantic with the centre of its distribution in Iceland. The world breeding population is estimated at *c.* 620,000 pairs, with at least 20% of these breeding in Britain and Ireland (Mitchell *et al.* 2004). As with many

seabirds, because a few colonies account for quite a large proportion of the population within Britain, and the importance of the British population within a biogeographical context, the Razorbill is Amber listed (Eaton *et al.* 2009).

Razorbills nest in boulder scree or on cliffs, but tend to prefer less exposed crevices and corners of ledges than guillemots. Razorbills begin to return to their colonies in January and February. Young birds return to the breeding colonies, spending progressively more time there and arriving progressively earlier, through age 2 to 5; they commence breeding in their fourth, or more commonly, fifth year of life.

Summary of recent estimates

Razorbills have been colour-ringed on the Isle of May for a number of years, and Harris *et al.* (2000) used re-sightings of individuals at the colony to estimate adult survival rates over a ten-year period. Similarly, Sandvik *et al.* (2005) used re-sighting data to estimate survival rates of Razorbills at a colony in Hornøya (Norway), who found significant heterogeneity between individuals, which may have biased survival rates significantly. There are also earlier estimates of survival from Skokholm/Skomer (Lloyd & Perrins 1977; Hudson 1979) and the Shiant Isles (Steventon 1979). The Skomer population was well studied (for other reasons), at least until recently, but no estimates of survival have been published.

Issues for estimating survival rates

Although immature birds show some movement between colonies before breeding (prospecting at alternative sites) studies have suggested that they tend to settle at their natal colony to breed. For example, only 3/477 (0.6%) birds re-trapped on Skokholm had been banded elsewhere (Perrins 1978). Site-faithfulness seems quite high in razorbills, with most pairs keeping the same site from season to season. Lloyd (1976) recorded site tenacity of over 90% with the majority of changes being associated with changes of mate (usually after the death of a partner). Harris & Wanless (1989) recorded 93% of colour-ringed birds breeding at same site in subsequent years. High site fidelity means that mark-recapture studies can provide a useful indicator of survival rates. Lloyd & Perrins (1977) suggested a small but variable proportion of adult birds did not breed each year. Harris & Wanless (1989) recorded 3% of colour-ringed birds that bred in one year not breeding the next. An additional problem is that the concealed nest sites will lead to relatively low re-sighting rates and may also induce fine-scale heterogeneity in re-sightings relating to nest-site exposure.

Razorbills appear to be truly migratory in the first two years of life, migrating further from the colony in their first winter than in subsequent years; from the third year onwards their distribution is more typical of a dispersal away from the breeding colonies (Wernham *et al.* 2002). As a result, adult and young birds face different temporal and spatial patterns of mortality and reporting probabilities, which would need to be taken into account when modelling survival rates.

4.4.5.3 Black Guillemot

Introduction

In Britain, the Black Guillemot, or Tystie, is largely restricted to the north and west coasts of Scotland and around the coast of Ireland (though there are few pairs breeding in the flatter southeastern counties, such as Waterford and Wexford). It is one of the more difficult seabirds to census as it tends to nest away from the main seabirds in small, dispersed colonies on small rocky islands or low-lying rocky coasts; nests also tend to be hidden in rock crevices or under boulders. Although populations are not declining in Britain and Ireland, the Tystie is

Amber listed (Eaton *et al.* 2009) because it is a species of European conservation concern (Burfield & van Bommel 2004) as up to half of the world population breeds in Europe.

Summary of recent estimates

Ewins (1988) estimated adult survival rates for Tysties breeding on Shetland, despite that fact that the probability of recovery was highly dependent on the frequency and timing of visits to the vicinity of the breeding colonies to search for corpses. Elsewhere, Frederiksen & Petersen (1999) analysed long-term adult survival rates of colour-marked population of Tysties breeding on Flatey in Iceland and found no evidence that these varied over time There was an apparent trend in survival of pre-breeding birds, but the possibility that this reflected heterogeneity in capture probabilities could not be excluded.

Issues for estimating survival rates

Because Tystie nests are usually hidden, it is often hard to locate, mark and follow a large sample of birds. This problem is exacerbated by their tendency to nest in relatively small colonies, so obtaining a sufficient sample size to provide useful estimates of survival rates will be difficult. However, once the chicks have hatched the adults can be seen carrying fish and tend to spend more time on rocks near the nest sites, when their rings can be read. Estimates of site-faithfulness in Tysties appear reasonably high after the first breeding attempt (over 70%). Of those birds that do change site the majority move to within 30m of the original site (Preston 1968, Asbirk 1979). However, this, combined with variable re-sighting effort among sub-colonies, can create problems with heterogeneity of resighting rates, as on Flatey (Frederiksen & Petersen 1999).

4.4.5.4 Puffin

Introduction

The smallest of our breeding auks, the Puffin is also our second commonest breeding seabird (after Guillemot), with about 10% of the European population breeding here. The species is Amber listed (Eaton *et al.* 2009) because of a localised population, and because the species is of conservation concern at a European scale due to a large decline in the 1970s and 1980s (Burfield & van Bommel 2004).

Puffins nest in colonies mainly on offshore islands but also on less accessible sections of mainland cliffs. They return to the colonies in mid-March to early April gathering in rafts on the sea first. They nest among boulders and down burrows, which they either excavate themselves or take over from rabbits or shearwaters. The puffin's life cycle differs from that of razorbills and guillemots in that chicks are reared underground until fully grown (about 6 weeks), and are independent of their parents at fledging (Harris 1976*b*, Harris & Birkhead 1985). Estimates of productivity are quite high with over 80% of breeding pairs fledging a chick (Isle of May, Harris 1983, Harris & Bailey 1992). However this value can be reduced to a mean production of 0.56 fledged young per pair, taking into account that as many as 30% of sexually mature adults may not breed in any one year (Harris 1983). Young puffins return to the colony at 2 or more usually 3 years old. They may breed at four years old but are usually not successful until 5 years of age (Ashcroft 1979, Harris 1984).

Summary of recent estimates

A long-term colour-ringing and re-sighting programme has been conducted for puffins on the Isle of May. Adults have been given numbered and colony specific colour-rings and pulli have been given year specific colour-rings, with survival rate estimates obtained from sightings of colour-ringed breeding adults and recaptures of birds ringed as chicks. A number

of studies have reported on the survival estimates obtained for adult and immature birds (e.g. Harris 1983; Harris & Bailey 1992, Harris & Rothery 1985, Harris *et al.* 1997a, 2005). Harris *et al.* (1997*a*) analysed the re-sighting data to allow for 'trap-dependence' where some burrows are consistently easier to observe and a bird is more likely to be re-sighted if it was seen or ringed the previous year than if it missed a year. More recently, Harris *et al.* (2005) showed that survival of Puffins at five colonies spanning their range in the eastern Atlantic was similar, and Harris *et al.* (2000b) showed that, for the Isle of May at least, that adult survival was closely related to the distribution and abundance of their prey (sprats). Long-term colour-ringing of Puffins has also occurred on Skomer (Poole *et al.* 1998) and Fair Isle. Elsewhere there are recent estimates of survival from Norway (Sandvik *et al.*2005) and Maine, USA (Breton *et al.* 2005). This latter study, again suggested there was little difference in survival rates between colonies (or, indeed, between years).

Issues for estimating survival rates

Immature Puffins often visit several colonies before settling (particularly in the July of their third year of life) and many may end up breeding away from their natal colony. Harris (1983) estimated that up to 23% of Puffins of both sexes permanently emigrated from their natal colonies. Other observational studies of the return of birds colour-ringed as chicks suggest the emigration rate may be as high as 46% (Harris 1976, Kress & Nettleship 1988, Harris & Wanless 1991). Some major long-distance movements have been recorded (*e.g.* a chick fledged on the Farne Islands has been found breeding in Norway), but the numerous short-distance movements which occur are more important in population dynamics (Harris 1984). Such movements may account for periods of colony growth, such as that seen on the Isle of May in the 1970s (Harris 1983). Inter-colony movements decrease as Puffins become established at a colony (Kress & Nettleship 1988), and once an adult has bred successfully, it rarely moves colony or even area (Ashcroft 1979). For example, Harris *et al.* (1997*a*) found no evidence of a bird ever occupying a burrow more than a few metres from the original one once it had bred.

Estimates of the frequency of adult non-breeding in the puffin are relatively high compared with many other seabirds: Harris (1983) estimates that on the Isle of May as many as 30% may abstain in any one year, and Ashcroft (1979) estimated that on Skomer each year 20-27% of adults were without nesting burrows and 5-16% of those birds with burrows did not lay. Such behaviour would need to be carefully accounted for in estimating survival rates as it may introduce heterogeneity in the re-sighting rates, with a consequent bias in survival rates.

In general, the puffin is a very pelagic bird. Outside the breeding season its habits remain a mystery with adults widely dispersed at low density throughout the North Sea (Harris 1984, Tasker & Pienkowski 1987, Stone *et al.* 1995). The recovery rate of ringed Puffins is relatively low (even for a seabird) at c. 1%. This low recovery rate is almost certainly because puffins spend most of their lives in areas where there is no-one to find the rings when they die (bodies may sink at sea and some birds may also die in burrows) (Harris 1984). As with other auks, young and old puffins tend to be recovered at different times and in different ways (Harris 1984). Wintering areas also vary by age and breeding colony leading to large-scale variation in the probability of recovery (Wernham *et al.* 2002). Results from ring recoveries suggest that, for example, 0.5% of rings placed on adult puffins on the Isle of May have been recovered, compared to only 0.2% of those placed on birds from St. Kilda, because birds from the former winter in the North Sea whilst birds from the later disperse further afield (Harris 1984).

4.5   Summary and recommendations

The amount of available data on seabird populations and hence the information and precision of survival rate estimates varies enormously between seabird groups, with highly detailed information at

multiple colonies available for some species, e.g. guillemot and kittiwake, but little or no survival information is available for some species, notably petrels and some gulls (see Table 5). In most of what follows, references to survival should be taken as to adult survival. In most cases, estimating survival of immature birds, or equivalently, recruitment of young birds into the breeding population on an annual basis is likely to be challenging (though see e.g. Harris *et al.* 1994b, 2007); despite the likely importance of this in determining population change.

Future work on survival rates will contribute to three main areas: research on topics of applied and/or academic interest, analysis of existing data and routine monitoring of survival rates on a more or less annual basis. Research projects have contributed, and will continue to contribute, enormously to our understanding of survival rates and population dynamics in seabirds. The long-running studies on the Isle of May have been particularly valuable in this regard as they have been able to build up detailed knowledge of demographic parameters (and their variability) over many years. Information from such projects could contribute to wider monitoring programmes, and information from such monitoring programmes can often provide valuable contextual information and even basic model parameter estimates for more focussed research programmes. Detailing such programmes is outside the scope of this report, so we will concentrate on the latter two subjects, namely, what current data holdings might be used for, and the scope for potential future monitoring of survival rates.

A major consideration in any monitoring programme is the amount of data required, we address this issue briefly below, but note here that to be effective, such monitoring needs to be able to achieve estimates on at least an annual basis to account for heterogeneity in ringing effort and annual fluctuations in environmental conditions. Consequently, such monitoring is only likely to be effective at relatively large colonies where a sufficient number of birds can be marked. Much effort has gone into developing analytical software to model survival rates efficiently and to account for various sources of heterogeneity in the data (e.g. programs MARK, White & Burnham 1999 and E-SURGE, Choquet *et al.* 2008). Such methods should be used where possible, but they do require relatively large samples of good quality data in order to estimate all the necessary parameters; they are best applied, and survival estimates are most robustly generated, where a structured network of sites exists in which ringing and (importantly) re-sighting effort are known.

Current availability of survival information

There has been a lot of past effort in ringing seabirds so there is a lot of pre-existing data that can usefully be analysed to provide information on patterns and trends in survival rates and the impacts of environmental drivers on these and population change. Because of its specialised nature seabird ringing tends to be undertaken by committed individuals, so there are many relatively long-running programmes at particular sites which should be encouraged to continue if possible; the value of such datasets increases greatly with their length, as has been shown time and again (*e.g.* Perrins *et al.* 1991). Marking to estimate survival rates requires a 'lead-in' time of 3-4 years before useful information can be generated, thus maintaining existing programmes is a cost-effective way of collecting data. In particular, marking programmes at the key sites in the Seabird Monitoring Programme (Isle of May, Skomer, Canna and Fair Isle) provide valuable data for a range of species which have been extremely important in developing our understanding of the environmental drivers of population processes in seabirds.

Many cliff-nesting species are well-suited to colour-marking studies, being relatively easy to capture, at least on the accessible fringes of the colony, and re-sight individuals (though it should be noted densely nesting species, such as auks can suffer from undue disturbance). This is evidenced by the number of long-running studies that have been undertaken or are ongoing on a range of species, such as Fulmar (Eynhallow), Gannet (Bass Rock), Guillemot and Kittiwake (Isle of May). Secure funding for long-term studies is always an issue and maintaining those studies that are already underway should be a priority (which applies equally to other species). Although the populations of many cliff-nesting species are broadly increasing, recent years have seen major breeding failures at a number of colonies related to climate-induced shifts in prey distribution (e.g. Kittiwake, Frederiksen *et al.* 2004).

If continued in future years these could have major impacts on the population structure, both through reduced productivity (sometimes catastrophically so) and, potentially, reduced survival as birds have to work harder to find food. Given the importance of the UK's seabird populations in a European context, further monitoring is essential, ideally on a regional basis, for example productivity of many species tends to differ between colonies on the North Sea and Atlantic coasts as the ecological conditions differ dramatically.

The cormorant is both a species of conservation interest (Britain supports internationally significant numbers in winter) and commercial interest (from interactions with anglers). There has been a long-term colour-marking programme on cormorants, which has yielded re-sightings of many birds. Consequently, good estimates of survival, and possibly also of dispersal, should be available, which would help explain patterns of population change in this important species and inform the debate on population management.

It is unclear how important Britain's storm-petrel populations are in an international context, mostly because of difficulties in censusing them, particularly in northern colonies, such as those on Iceland or the Faroe Islands where large numbers are thought to breed. Even within Britain and (especially) Ireland, they are logistically quite difficult to study, occurring on remote islands and being largely nocturnal. It can also be difficult to determine which individuals that are caught are actually breeding at a particular colony, as they can wander quite widely. Catching during May (Leach's Storm-petrel) or mid-May to mid-June (European Storm-petrel) may reduce the number of non-breeding wanderers caught as these, apparently, tend not to visit colonies until later in the year (Fowler *et al.* 1986; Insley *et al.* 2002). Consequently, storm-petrels are probably not a high priority for survival monitoring, even though (or perhaps because) so little is known about their biology or population trends.

Manx Shearwaters, on the other hand, although nocturnal and confined to islands in the west of Britain, have been the subject of a number of long-running studies, notably on Rum, Skomer, Bardsey, Copeland and Canna; this latter is a RAS study. In an international context the British and Irish populations are of huge significance, representing around 90% of the world population. Population trends are difficult to ascertain because of the lack of sufficiently detailed historical censuses, although the limited data that are available suggest populations are stable or declining. This situation should improve in future using the Seabird 2000 counts as a baseline (Mitchell *et al.* 2004). Given the uncertainty in population trend and the availability of ringing data from several colonies an analysis of survival rates using mark-recapture data from these colonies, and possibly the ring-recovery data should be a relatively high priority. Combining this analysis with productivity information from these colonies, where it is available may also yield useful insights into the population trends of this Amber listed species.

Monitoring survival of the two breeding skuas is likely to be possible at least at some colonies, notably Foula (e.g. Ratcliffe *et al.* 2002, Davis *et al.* 2007). While for Arctic Skua, relatively few sites will hold sufficient numbers of birds to provide useful annual survival estimates from mark-recapture studies, the potential for a network of sites to monitor Great Skuas is high, as a number of colonies hold large numbers of birds. There is an ongoing study on Foula and data from Hermaness and Handa (although these studies are no longer operating). Such monitoring would be particularly important as Britain (Scotland) holds about 60% of the world population of Great Skua.

Given how common most gull species are, it is perhaps surprising how few studies of survival rates there have been. Probably the most important omission in this regard is Herring Gull, which is now Red-listed because of recent population declines, particularly in coastal populations. Such an analysis could focus on the differences in survival between coastal and urban populations, which should reveal the demographic differences causing inland populations to be increasing, while coastal populations decline. Similarly, much could be learned from a comparative analysis of Lesser-black Backed Gull survival rates; in many ways they have a similar ecology, though there are some important, and instructive, differences, notably that the blackback population is increasing. There are or have been several colour-ringing studies on these species (notably in Cumbria, Essex and in the Severn basin)

which have generated many re-sightings. Such an analysis should be considered a high priority, and could be usefully extended to include productivity information into an integrated population model. Survival rate estimates for other gull species would be useful (there are none currently for Great Black-backed Gull for example, although a recent colour-ringing scheme has been initiated in Essex). These are perhaps less of a priority, although both Common and Black-headed Gulls have declined moderately in recent years.

Estimating national survival rates for any of the tern species is problematic, because of the sometimes ephemeral nature of their breeding colonies, their perceived sensitivity to disturbance and the paucity of recoveries from their wintering grounds. Survival rate estimates would have to be generated using multi-site models that can take account of dispersal, such as is currently being undertaken for Roseate Tern (Ratcliffe *et al.* 2008). Similar analyses for other species would be useful, but there is less in the way of pre-existing long-term data (requiring new studies) and a critical evaluation of such data would be needed prior to starting.

Amongst the auks, there is much work underway on Guillemot and Puffin populations, notably on the Isle of May and Skomer, though less on Razorbills and Black Guillemots. Consequently, there are good estimates of annual survival available for the former two species, although from only a few colonies. Studies at other colonies should be encouraged to help understand regional differences in survival (though it is unclear whether these exist in the case of Puffin) but are of low priority. Estimates of survival for Razorbill and Black Guillemot are currently less satisfactory, but will require significant extra data collection to improve.

This is perhaps a higher priority for Black Guillemot as survival rate estimates may help in estimating population trends, given the difficulties in censusing this species accurately; it would make a good candidate for study under the RAS program, if sufficient numbers of adults could be marked.

Analyses with current data

Because of the high public and volunteer interest in seabirds much data has already been gathered on seabird survival rates and, although some analyses have been undertaken, there remains much that could usefully be done. In this regard, three analyses largely utilising existing datasets seem particularly useful:

o There are a number of long-running mark-recapture studies on Manx Shearwater and some recovery information. Given the high proportion (>75%) of the world population that breeds in the United Kingdom and the lack of any information on population trend in this species an analysis of ring-recapture and recovery data from existing studies would seem to be a high priority in understanding the status of this species.

o The spread of Cormorants inland, immigration of birds from Europe and their use of angling lakes, has created much controversy. There is widespread mark-resighting data for this species allowing us to investigate differences in its demography between regions and the two subspecies, which have different population trajectories. This should be directed at understanding the impacts of any population management strategies, particularly on the Amber-listed *P. c. carbo* subspecies.

o Herring and Lesser Black-backed Gulls share some similar ecological traits but are exhibiting very different population trends; herring gull populations, particularly those in coastal regions are declining, while Lesser Black-back populations are increasing. Both species are rapidly increasing their use of urban areas with potential public health consequences. There is much ring-resighting data for both species and an analysis of this data should yield many interesting insights into the population ecology of these species.

Information from currently available data can also be used to provide basic information in terms of parameterising population models, in which case strictly annual estimates of survival rates may not be required. In this latter regard, relatively straightforward analyses of some species, such as Great Black-backed Gull, for which there appear to be no published survival rate estimates, may be useful.

Future Monitoring

From the foregoing it can be seen that analysing seabird survival rates is relatively complex with a lot of factors to be considered. These complexities stem largely from the fact that seabirds are long-lived, generally breed colonially in terrain that is difficult to sample uniformly and often occur in places far from human activity. In order to produce useful estimates of survival rates many of these factors need to be accounted for analytically. Focussed colour-ringing of individuals is likely to provide, in many cases, sufficient sample sizes as the re-encounter rate is much higher than for simple dead recoveries. It also removes the need to recapture birds, which can be exceedingly difficult in some case. However, they can suffer from the problem of estimating emigration. For this reason an analytical approach using both types of data is to be preferred. To achieve this would require a geographically dispersed network of a small number of sites (per species) where sustained (colour-)ringing effort could be maintained. Running such a network could be done very cost-effectively using volunteer seabird ringers. However, some thought would need to be given to appropriate training as such specialised ringers are currently relatively few in number and also to developing the necesarry re-sighting programmes in a manner that is sustainable over a number of years. The major costs would come in the analysis of data, which would require analysts who were very familiar with this type of data.

Because of their colonial nature and specialised breeding habits, many sites could actually function as part of a network for several species, obvious examples include Fair Isle, the Isle of May, Skomer and Foula. Of these, the first three are currently key monitoring sites within the SMP program. These sites are of critical importance and the results of ringing the programmes on the Isle of May and Skomer (particularly) have been extremely important in furthering our understanding of seabird biology and the impacts of fishing marine pollution and climate change on population status and change. Expanding this network of sites and facilitating colour-marking of species at sites geographically representative of their whole range in Britain is probably the most effective way of monitoring seabird survival. Substantial resources, however, would need to be available to manage re-sighting effort and analyse the data subsequently. Colour-marking studies will, however, necessarily be limited to a few sites, which will make estimating pre-breeding survival difficult (due to extensive natal dispersal). Consequently, there is still likely to be a role for metal ring-recovery analyses particularly when combined with re-sighting data from colour-marked studies in joint analyses.

In many ways, seabirds make ideal study species for projects within the Re-trapping Adults for Survival (RAS) scheme, for example, large numbers of birds breed in relatively discrete location; they are highly site-faithful with adults returning to the colony in most years and re-trapping (or re-sighting) marked birds is possible. Indeed, there are already a number of RAS studies focussing on seabirds, notably three on Storm Petrels, two on Kittiwakes and a long-running study on Manx Shearwaters. This might be particularly true of smaller colonies where, over time, a substantial proportion of adults in the colony can be marked. Priority species for establishing such a network of sites (in the sense of species suited to the RAS methodology) would include fulmar, Manx shearwater, shag, kittiwake, arctic skua and possibly guillemot, though with last species issues of disturbance at the colony would need to be especially considered. For all of these species good colour-marking studies are already in operation so establishing new study areas is in principle feasible and likely to yield good results. These species also encompass a range of seabird ecologies and does overlap with those species identified as priorities for annual monitoring in the SMP surveillance strategy (fulmar, gannet, shag, kittiwake, razorbill and guillemot, Way & Mitchell (2008)). Because adults are difficult to catch cormorants would not make a good RAS species, but their survival can be monitored through the extensive colour marking of birds that currently exists.

Generally, a relatively low proportion of seabirds are ringed as adults, particularly on the breeding grounds. There are good numbers of adult gulls ringed in the winter, mostly on landfill sites, but since these birds are likely to have multiple origins and many, if not the majority may breed in other countries, their utility in monitoring British breeding populations is limited (Wernham *et al.* 2002).

Additional ringing of adult birds at breeding colonies, where possible, is therefore to be encouraged. In principle, one would conduct a power analysis to try and estimate the additional number of adult birds to be ringed to be able to provide survival rate estimates of a given precision. However, this is unlikely to be straightforward as the precision of survival rate estimates is more affected by the number, and particularly the patterning between years, of recaptures. In principle ringing effort which would generate 30-50 recoveries per year should be regarded as a minimum to generate usefully precise estimates of annual survival (Robinson *et al.* 2007). Given a recovery rate of 2-3% this would mean ringing in the region of 1,000 to 2,000 adults a year, which may be unrealistic for some species. However, combining recoveries with mark-recapture studies (where re-encounter rates are typically much higher) should reduce this number considerably. In practice, the number of adults likely to be ringed will be constrained by the number catchable within a given time such that disturbance at the colony is minimised.

5.   INTEGRATED POPULATION MODELLING

Clearly, population trajectories are influenced by a combination of demographic parameters, notably productivity (Chapter 3) and survival (Chapter 4), though in some species, e.g. terns, movements between populations may also have to be taken into account. Thus, to determine causes of population change information on both demographic parameters is required because populations may not be equally sensitive to, or affected by, each parameter.

5.1   Sensitivity of seabird abundance to life-cycle stages

Optimal life history strategies for seabirds demand that they maintain high adult survival rates and vary reproductive output in response to fluctuations in food availability (Cairns 1987). Adult survival will therefore tend to be stable over time, while productivity will vary much more, a pattern found in several studies of seabirds faced with annually variable food availability (Monaghan *et al.* 1992, Hamer *et al.* 1991, Pons and Migot 1995, Nur and Sydeman 1999). It seems logical then, that productivity is the most important variable to measure in any monitoring scheme, as this is the most variable and will therefore contribute more of the variance in population trends. However, this ignores the fact that the sensitivity of population trends to a given percentage change in demographic parameters is not constant (Lebreton *et al.* 1991). Sensitivity analyses are required to determine the changes in population size caused by a given percentage alteration in age-specific survival and productivity.

Croxall and Rothery (1991) performed such sensitivity analyses for two hypothetical seabird species that represent the extremes of the life history strategies found in seabirds. Species P had a high survival of 0.95, a productivity of 0.30 female chicks per pair, an age of first breeding of 5 years and a low survival to recruitment of 0.17. These demographic parameters are typical of petrels, auks and gannets. Species S had a lower adult survival rate of 0.80, an age of first breeding of three years, a productivity of 0.6 and higher survival to recruitment of 0.33; characteristics representative of cormorants, gulls and terns.

The results of the simulations are presented in Table 4. This shows that in both species, population trends are extremely sensitive to a change in adult survival rate; populations of species P would decline by 4.2% in response to a 5% decline in adult survival, and this effect would be manifested in the following year. In contrast, a 5% decline in productivity would only produce a decline of 0.8% in the breeding population size, and that would occur five years after the event. Species S is less sensitive to changes in adult survival and more sensitive to those in productivity. However, even this species, population size is almost 3 times more sensitive to a given change in adult survival than in productivity. Seabird populations are clearly extremely sensitive to changes in adult survival, so changes in other demographic parameters required to compensate for small declines in adult survival are therefore large. For example, in species P, a decline in survival by 5% would require a doubling in productivity to maintain a stable population, which may not be possible if the species were only able to lay a single egg. This highlights the limited capacity of seabird populations to buffer small changes in survival rates via density dependent changes in productivity.

The sensitivity of seabird population trends to small changes in adult survival rates makes populations vulnerable to reductions in this parameter (Birkhead and Furness 1985, Croxall and Rothery 1991). Reduced survival may take the form of a small, but long-term, reduction that will produce a chronic population decline (Weimerskirch and Jouventin 1987, Croxall *et al.* 1990), or a stochastic catastrophe in which a single large mortality incident produces a population crash (Potts *et al.* 1980). Density-dependent increases in productivity or recruitment have limited capacity to compensate for these changes (Croxall and Rothery 1991), and may take years to be manifested because of the tendency to defer breeding. The low recruitment rate of seabirds means that the populations will be slow to recover after the reduced survival is mitigated (Weimerskirch *et al.* 1997).

To put this into the context of quantitative conservation concern criteria, the changes in demographic rates required to that would produce population declines at a rate that would qualify a species for inclusion on the Red List of Birds of Conservation Concern (50% over 25 years) were investigated. Population trajectories for species S and P were simulated over 25 years with a focal demographic parameter varied iteratively to produce a 50% decline over 25 years, whilst holding the values of other parameters constant (Croxall and Rothery 1991). These simulations demonstrated that a reduction in mean annual adult survival over the period of 3.14% for species P and 3.66% for species S would be sufficient to produce a population decline at a rate that would qualify each for inclusion on the Red List (Table 4b). Survival to recruitment and would need to change by around 9% for species P and 6% for S and annual productivity would need to show a 10% decline over the period for both species. Thus, monitoring adult and juvenile survival rates as well as productivity is required if effective diagnosis of seabird population declines is to be achieved.

The challenge for seabird population ecologists is to produce survival estimates that are sufficiently precise that such small changes in adult and juvenile survival rates can be identified. The precision (standard errors) would ideally need to less than 5% of the estimate for adult survival and less than 10% for immature survival in order to implicate changes in these parameters as the cause of a long-term decline. It is difficult to calculate, a priori, to estimate the numbers of birds needed to be ringed to obtain estimates with this level of precision, particularly when there may be heterogeneity between sites to account for. However, Robinson et al. (2007) estimated that, for waders, a minimum of 100 re-encounters per year per site would be required. Frederiksen et al. (2004a) achieved this sort of precision for adult Kittiwakes by colour-marking 500 birds, of which around 150 were re-encountered annually. Harris et al. (2000a) estimated survival rates of breeding Puffins using metal-ring captures and colour-ring re-sightings. The re-sighting study (Isle of May) involved 600 birds, of which 300 were seen annually, this lead to a precision on annual estimates of 1-2%. Mark-recaptures required larger numbers of birds ringed, with one handling annually 500 birds (Canna) achieving a precision of 3-5% and that handling 100 birds annually (Colonsay) failing to estimate annual rates in many years. So clearly, large colonies and a moderate degree of effort are likely to be required in order to obtain useful estimates.

Although, one ideally requires quite precise estimates of survival rates; that is not to say that estimates of lower precision are worthless. Seabirds populations are often subject to catastrophic mortality events (e.g. Potts et al. 1980, Coulson and Strowger 1999) that can be may be an important aspect of seabird population regulation (Croxall and Rothery 1991). The influence of these events on overall population trends is dependent on their frequency and magnitude and this could be adequately monitored with survival estimates that are less precise than the levels specified above, as has been the case for knot *Calidris canutus* (Atkinson et al. 2003). Also, density-dependent increases in breeding success and earlier ages of first breeding are likely to partially compensate population declines caused by reduced survival (Croxall et al. 1990) and so the actual changes in survival required to produce a Red Listed decline would be slightly larger than this simple simulation exercise indicated. On the other hand, adult and juvenile survival are likely be affected by similar external factors if the geographic distributions of the age-classes within a species is similar. If survival at different ages were reduced in tandem rather than independently as assumed in the above analysis, a rate of decline onto the Red List could be produced by reductions in each parameter that are smaller than those presented.

5.2   Models of Demography and Populations

A key aim of the BTO's Integrated Population Monitoring programme is to understand the demographic causes of population change (Baillie 2001). To date, this programme has been very successful, with population models produced for a number of species, particularly passerines of conservation concern (e.g. Reed Bunting *Emberiza schoeniclus* [Peach et al. 1999], Song Thrush *Turdus philomelos* [Robinson et al. 2004] and Starling [Freeman et al. 2007]). However, these analyses have largely been done piecemeal, that is, each data set has been modelled in isolation and the results of these analyses combined to produce the overall population model. Combining such

datasets results in much greater analytical power, both because the statistical errors can be estimated more accurately, but also because each dataset, in principle, contributes information to understand the others (for example, populations are likely to be smaller following years when survival is likely to be low). Such combined models require computationally intensive methods, but recent advances, both through using approximations such as the Kalman Filter (Besbeas & Freeman 2006, Besbeas *et al.* 2002, 2003) and, more recently, using Bayesian methods (e.g. Brooks *et al.* 2002, 2004; Reynolds *et al.* in press) have greatly increased the ease with which such models may be used. Bayesian methods have the additional advantages that information can be combined from a number of sources (in particular 'prior' information can be incorporated) and that model predictions include a direct measure of the certainty of predictions, enabling various different modelling scenarios to be reliably compared.

Although there is much interest in seabird populations, demographic models are relatively few, and mostly use simple matrix projection models, employing average values for the demographic parameters (e.g, Hunter *et al.* 2000; Frederiksen *et al.* 2004; Oro *et al.* 2004), although a population model of (primarily Scottish colonies of) Guillemots using a Bayesian framework has been constructed (Reynolds *et al.* 2009). This study is important in that it showed that by combining all the demographic information, one could improve estimates of each parameter and even estimate quantities for which one had little direct data, such as juvenile dispersal. There are a number of challenges to constructing such models, not least of which is the availability of data, and the need for such populations to be age-structured. Although age-structured population models have been fitted (e.g. Brooks *et al.* 2004), these have generally been for two age-classes. For long-lived seabirds, which do not breed until they are 4-6 years old (depending on species), several age-classes are likely to be required to model population processes accurately, increasing the number of parameters to be estimated, and for which there are likely to be little data. Of course, it may be possible to combine some age-classes to estimate combinations of parameters that may be confounded by lack of data anyway, and, in many cases, estimating recruitment into the breeding population of fledged birds may be the key demographic parameter. Integrated modelling, particularly using Bayesian approaches, may be most useful where complicated models are required, such as where there is significant movement of birds between colonies between years, for example in modelling populations of terns and shag.

Although truly integrated population modelling is likely to represent the way forward in understanding population changes in the longer term, that is not to say that much useful work can not be done using simpler methods, i.e. looking at demographic trends individually, both in terms of monitoring population status, and in understanding reasons for population change (*e.g.* Frederiksen *et al.* 2004a).

As can be seen above, changes in survival are likely to have greater population impacts on seabirds than annual variation in productivity. The relative importance of one-off catastrophic mortality and longer-term changes, perhaps because of changes in prey availability, in determining population change is likely to vary between species and the spatial variation in mortality. Clearly, though, it is likely to be easier to detect large but short-term changes in survival than smaller changes over the longer term, which will require much higher quality data.

5.3 Priorities for Population Modelling

Table 5 provides a broad indication of species for which population modelling is likely to be possible, and to provide useful information.

For some species, notably Red-throated Diver and Great Black-backed Gull, there is little data on which to construct population models, and little likelihood of being able to collect sufficient appropriate data, so these species may essentially be disregarded. Great Skua represents almost the other end of the spectrum. Because of intensive studies at the major colonies, which are relatively few in number, much is known about the numbers and population processes in this species and formal populations are likely to be highly informative, as they can use much pre-existing data, perhaps in

predicting patterns of future spread, which may have important consequences for other seabird populations (Votier *et al.* 2004).

On the other hand, relatively good data is available for many of species, at least in terms of productivity and survival; some assumptions may still have to be made about other demographic parameters, such as the proportion of birds breeding in a year and detailed differences in age-specific survival rates. In Table 5 we highlight some species for which population modelling should provide insights into population changes.

Britain holds a high proportion of the world's Manx Shearwater population, yet relatively little is known about its population dynamics. However, there should be sufficient information on productivity and survival, particularly given the existence of RAS studies on this species (albeit a small number). An analysis of survival and productivity trends over time would help understand population dynamics in this important species.

Cormorants are an important species given their interactions with man, particularly with angling interests, and proposals for culling individuals (e.g. Newson 2000). There is much good data on cormorant productivity and survival, particularly through a long-term co-ordinated colour-ringing programme. An integrated population model would provide further insights into the population spread of this species and help assess the population impact of any culling programme.

Herring Gulls have recently undergone a significant population decline, though the reasons for this are unclear. There is good data on survival from both colour-marking projects and national ring-recovery data, a combined analysis of which should allow good estimation of age-specific survival rates. There are also a data from (a relatively small) number of colonies which would allow estimates of productivity. An integrated population analysis would shed some light on the demographic reasons for the decline in this species (of which Britain holds about 20% of the biogeographic population). It would be particularly instructive to do this analysis in comparison with Lesser Black-backed Gulls, for which there are similarly good data, but which is increasing in population numbers, despite a broadly similar ecology in Britain.

Integrated population models may be particularly useful for modelling population dynamics of tern species, since they allow data from disparate sources to be combined in a single analysis. The best data are likely to be available for Roseate Terns and which are of highest conservation concern (though even for this species ecological and sampling issues may preclude a successful analysis), but studies of Sandwich Tern may also likely be feasible.

Amongst the auks there is a good amount of data on demographic processes in Guillemots and Puffins, but virtually none on Black Guillemot. There is thus potential for creating population models for the former two species, both of which could be used as indicator species of the marine environment. Indeed, development of integrated population modelling of Guillemots (within a Bayesian framework) is being undertaken as part of a three year research PhD (Reynolds *et al.* in press); development of such models is likely to take similar levels of effort.

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Table 1 Britain's seabirds. Species are categorised by broad ecological/taxonomic group. Breeding population size (number of pairs) in 2000 is taken from (Mitchell *et al.* 2004) and Biogeographical Importance refers to the proportion of the appropriate biogeographical population that occurs in Britain. Conservation Status is taken from Eaton *et al.* (2009).

	Group	Breeding Population	Importance	Status
Northern Fulmar *Fulmarus glacialis*	Cliff nester	540,000	17	Amber
Manx Shearwater *Puffinus puffinus*	Petrel	330,000	92	Amber
European Storm-Petrel *Hyrobates pelagicus*	Petrel	125,000	34	Amber
Leach's Storm-Petrel *Oceanodroma leucorhoa*	Petrel	48,000	1	Amber
Northern Gannet *Morus bassanus*	Cliff-nester	260,000	68	Amber
Great Cormorant *Phalacrocorax carbo*	Cliff-nester	14,000	23	Amber
European Shag *Phalacrocorax aristotelis*	Cliff-nester	32,000	47	Amber
Arctic Skua *Stercorarius parasiticus*	Gull	2,100	10	Red
Great Skua *Catharacta skua*	Gull	9,600	60	Amber
Black-headed Gull *Larus ridibundus*	Gull	140,000	6	Amber
Common Gull *Larus canus*	Gull	50,000	10	Amber
Lesser Black-backed Gull *Larus fuscus*	Gull	120,000	68	Amber
Herring Gull *Larus argentatus*	Gull	150,000	20	Red
Greater Back-backed Gull *Larus marinus*	Gull	20,000	19	Amber
Black-legged Kittiwake *Rissa tridactyla*	Cliff-nester	420,000	15	Amber
Sandwich Tern *Sterna sandvicensis*	Tern	14,000	20	Amber
Roseate Tern *Sterna dougallii*	Tern	790	37	Red
Common Tern *Sterna hirundo*	Tern	15,000	5	Amber
Arctic Tern *Sterna paradisaea*	Tern	55,000	7	Amber
Little Tern *Sterna albifrons*	Tern	2,200	11	Amber
Common Guillemot *Uria aalge*	Cliff-nesting Auk	1,600,000[1]	37	Amber
Razorbill *Alca torda*	Cliff-nesting Auk	220,000[1]	27	Amber
Black Guillemot *Cepphus grylle*	-	43,000[1]	10	Amber
Atlantic Puffin *Fratercula arctica*	Cliff-nesting Auk	600,000	10	Amber

[1] Individuals (for Black Guillemots of pre-breeding adults)

Table 2　　Current monitoring of seabird abundance and breeding success in the UK. Conservation priority was determined from a combination of population status, trend and importance of the UK population in an international context. Adapted from Mitchell & Parsons (2007), which see for full details.

		Abundance		Breeding Success	
	Priority	Sampling	Feasibility	Adequacy	Feasibility
Red throated Diver	High	Poor	Moderate	National	High
Northern Fulmar	Low	National	High	National	High
Manx Shearwater	Medium	Regional	Moderate	Regional	Moderate
European Storm-Petrel	Low	Poor	Low	Poor	Low
Leach's Storm-Petrel	High	Poor	Low	None	Low
Northern Gannet	Medium	Regional	Moderate	Regional	Moderate
Great Cormorant	Low	National	High	Regional	Moderate
European Shag	High	Regional	High	National	High
Arctic Skua	High	National	High	National	High
Great Skua	Medium	National	High	National	High
Black-headed Gull	Medium	Regional	Moderate	Regional	Moderate
Common Gull	Medium	Regional	High	Poor	Moderate
Lesser Black-backed Gull	Medium	Regional	High	Regional	Moderate
Herring Gull	High	Regional	High	Poor	Moderate
Greater Back-backed Gull	Low	Regional	High	Poor	Moderate
Black-legged Kittiwake	Medium	National	High	National	High
Sandwich Tern	Low	National	High	National	High
Roseate Tern	High	National	High	National	High
Common Tern	Low	National	High	Regional	Moderate
Arctic Tern	Low	National	Moderate	National	High
Little Tern	High	National	High	National	High
Common Guillemot	Low	National	High	National	Moderate
Razorbill	Medium	National	High	Poor	Low
Black Guillemot	Low	Regional	Moderate	Poor	Low
Atlantic Puffin	Low	Poor	Low	Poor	Moderate

Table 3   Average number of seabirds ringed each year (2000-2006) at colonies where more than 100 birds are ringed (on average) in a year.

Site	Fulmar	Manx Shear	Gannet	Shag	Arctic Skua	Great Skua	Guillemot	Razorbill	Tystie	Puffin	TOTAL
Sule Skerry	270	0	14	267	0	1	506	25	0	7491	8577
I. Canna	37	0	0	511	0	1	2165	202	0	18	2936
I. May	48	0	0	1089	0	0	662	27	0	722	2551
Sanda I.	45	92	0	381	0	0	1354	513	9	7	2403
Fair Isle	86	0	20	378	40	112	886	436	9	131	2101
Bardsey	2	1508	0	16	0	0	99	223	0	2	1852
Copeland	0	1218	0	0	0	0	0	0	25	0	1243
Lunga	26	1	0	93	0	0	501	92	0	309	1024
Hallival	0	905	0	0	0	0	0	0	0	0	905
Castle Craig	4	0	0	146	0	0	705	21	0	0	878
Puffin I.	2	0	0	254	0	0	99	134	0	1	491
Craigleith	82	0	0	188	0	0	27	46	0	119	465
Great Saltee	0	0	308	100	0	0	25	6	0	0	441
Swona	292	0	0	20	0	1	11	41	13	9	390
Faraid Head	16	0	0	19	0	0	222	78	0	5	341
Sule Stack	0	0	328	0	0	0	0	0	0	0	328
Ceann Ousdale	0	0	0	0	0	0	288	0	0	0	289
Calf of Man	0	49	0	169	0	0	0	13	0	0	233
Skomer I.	0	96	0	0	0	0	56	17	0	56	226
Y. Gwylan	0	0	0	101	0	0	43	4	0	30	179
Lady Isle	0	0	0	178	0	0	0	0	0	0	178
Badbea	3	0	0	152	0	0	0	7	1	0	164
Staple I.	0	0	0	158	0	0	0	0	0	2	160
Inchkeith	87	0	0	62	0	0	0	2	0	5	158
Leac Buidhe	6	0	0	5	0	0	81	53	0	6	154
Bride's Ness	137	0	0	0	0	0	0	0	1	0	138
Hermaness	0	0	67	2	0	20	0	27	0	4	122
Garbh E.	1	0	0	3	0	0	24	41	0	38	109
Hermaness	0	0	24	0	0	84	0	0	0	0	108
Shiant I.	0	0	0	9	0	0	0	61	0	33	104
Others	557	173	172	662	86	218	399	85	129	35	2521
	1707	4046	936	4974	126	441	8161	2164	190	9032	31782

Table 4.   Sensitivity of seabird species to demographic parameters.

	Parameter	Species P	Species S
a)	Adult Survival	4.2%	3.6%
	Survival to recruitment	1.5%	2.4%
	Productivity	0.8%	1.3%

Long-term population declines associated with a reduction of 5% in the specified demographic parameter in two hypothetical species of seabird (from Croxall and Rothery 1991).

	Parameter	Species P	Species S
b)	Adult Survival	3.14	3.66
	Survival to recruitment	8.87	6.00
	Productivity	17.10	10.45

The changes in demographic parameters required to cause a long term decline of 50% over 25 years and place each species on the Red List of Birds of Conservation Concern.

Table 5 Suggested ranked priorities for constructing integrated population models for seabirds. Species are considered of Moderate or High conservation importance if they are listed on the red and amber lists, respectively of Eaton *et al.* (2009). Data availability indicate the potential of being able to produce some form of annual/region estimates ('Good'), whether the likely available data will only support less robust measures (Moderate) or provide only very basic demographic information (Poor). The suggested priorities in the final column indicates species for population modelling is likely to yield most insight, based on likely data availability.

	Conservation Importance	Data Availability Productivity	Survival	Priority
Red throated Diver	Moderate	Moderate	None	Low
Northern Fulmar	Moderate	Good	Moderate	Moderate
Manx Shearwater	Moderate	Moderate	Good	High
European Storm-Petrel	Moderate	Poor	Poor	Low
Leach's Storm-Petrel	Moderate	None	Poor	Low
Northern Gannet	Moderate	Moderate	Good	Moderate
Great Cormorant	Low	Moderate	Good	High
European Shag	Moderate	Good	Moderate	Moderate
Arctic Skua	High	Good	Good	Moderate
Great Skua	Moderate	Good	Good	Moderate
Black-headed Gull	Moderate	Moderate	Moderate	Low
Common Gull	Moderate	Moderate	Poor	Low
Lesser Black-backed Gull	Moderate	Good	Good	High
Herring Gull	High	Poor	Good	High
Greater Back-backed Gull	Moderate	Poor	None	Low
Black-legged Kittiwake	Moderate	Good	Good	Moderate
Sandwich Tern	Moderate	Good	Moderate	High
Roseate Tern	High	Good	Moderate	High
Common Tern	Moderate	Moderate	Moderate	Moderate
Arctic Tern	Moderate	Good	Moderate	Moderate
Little Tern	Moderate	Good	Good	High
Common Guillemot	Moderate	Good	Good	High
Razorbill	Moderate	Poor	Moderate	Moderate
Black Guillemot	Moderate	Poor	Poor	Low
Atlantic Puffin	Moderate	Poor	Good	Moderate