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Subject: Hornsea Project Three (UK) Ltd response to Deadline 6 (Part 4)

Dear Kay, K-J

Please find attached the 4th instalment of documents.

Best regards,
Dr Dominika Chalder PIEMA
Environment and Consent Manager

███████████

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Hornsea Project Three

Offshore Wind Farm

Appendix 10 to Deadline 6 submission – Horsewill and Robinson 2015

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Front cover picture: Kite surfer near a UK offshore wind farm © Ørsted Hornsea Project Three (UK) Ltd., 2019.

**JNCC Report
No: 552**

**Review of Seabird Demographic Rates
and Density Dependence**

Catharine Horswill[1] & Robert A. Robinson[1]

February 2015

[1]British Trust for Ornithology

Summary

Constructing realistic population models is the first step towards reliably assessing how infrastructure developments, such as offshore wind farms, impact the population trends of different species. The construction of these models requires the individual demographic processes that influence the size of a population to be well understood. However, it is currently unclear how many UK seabird species have sufficient data to support the development of species-specific models.

Density-dependent regulation of demographic rates has been documented in a number of different seabird species. However, the majority of the population models used to assess the potential impacts of wind farms do not consider it. Models that incorporate such effects are more complex, and there is also a lack of clear expectation as to what form such regulation might take.

We surveyed the published literature in order to collate available estimates of seabird and sea duck demographic rates. Where sufficient data could not be gathered using UK examples, data from colonies outside of the UK or proxy species are presented. We assessed each estimate's quality and representativeness. Estimates are usually only available for a limited number of colonies, and there may be substantial inter-colony variation. Therefore we also indicate the extent to which estimates may be applied to different colonies.

This report and the accompanying material details demographic information on the 32 species of seabird and sea duck thought to be most vulnerable to off-shore renewable developments in the UK. The species covered are (in taxonomic order): greater scaup (*Aythya marila*), common eider (*Somateria mollissima*), goldeneye (*Bucephala clangula),* long-tailed duck (*Clangula hyemalis)*, common scoter (*Melanitta nigra*), velvet scoter (*Melanitta fusca*), red-throated diver (*Gavia stellata*), black-throated diver (*Gavia arctica*), great northern diver (*Gavia immer*), Manx shearwater (*Puffinus puffinus*), northern fulmar (*Fulmarus glacialis*), great cormorant (*Phalacrocorax carbo*), European shag (*Phalacrocorax aristotelis*), northern gannet (*Morus bassanus*), great crested grebe (*Podiceps cristatus*), Arctic skua (*Stercorarius parasiticus*), great skua (*Stercorarius skua*), black-legged kittiwake (*Rissa tridactyla*), little gull (*Larus minutus*), black-headed gull (*Chroicocephalus ridibundus*), common gull (*Larus canus*), lesser black-backed gull (*Larus fuscus*), herring gull (*Larus argentatus*), great black-backed gull (*Larus marinus*), Sandwich tern (*Sterna sandvicensis*), common tern (*Sterna hirundo*), Arctic tern (*Sterna paradisaea*), little tern (*Sternula albifrons*), common guillemot (*Uria aalge*), razorbill (*Alca torda*), black guillemot (*Cepphus grylle*), Atlantic puffin (*Fratercula arctica*).

The drivers that cause year-to-year variation in survival and productivity rates and the direction of their influence are also presented. In the majority of species this demonstrates that information on a specific colony cannot necessarily be extrapolated to multiple colonies without applying some degree of qualitative interpretation.

The majority of the seabird species considered received high and intermediate data quality and representation scores for adult survival rates. The exceptions were great black-backed gull and little gull. There was considerably less information available on juvenile and immature survival rates, and great northern diver, northern fulmar, Arctic skua, common tern, razorbill and Atlantic puffin were only available as return rates between fledging and recruitment. Juvenile and immature survival rates were not available for goldeneye, long-tailed duck, velvet scoter, Manx shearwater, little gull, black-headed gull, great black-backed gull, Arctic tern and little tern. An estimate of productivity from a long-term monitoring study was identified for the majority of species, with the exception of little gull. However, in some

species this was only available for a limited number of species. The survival and productivity rates of sea ducks were largely lacking, with the exception of common eider.

An estimate for age of recruitment was available for all of the seabird and sea duck species considered. There was considerably less information identified for the incidence of missed breeding and the rate of breeding dispersal (both of juveniles and adults). Elevated rates of natal dispersal were identified in northern fulmar, black-legged kittiwake, common gull, lesser black-backed gull, herring gull, arctic tern, common guillemot and black guillemot. However, these processes are likely to vary between colonies. Therefore the reported rates should not be used without applying some degree of qualitative interpretation.

There was substantial evidence that populations of seabirds and sea ducks exhibit compensatory density-dependent regulation on survival, productivity, recruitment and dispersal processes. However, in specific species and populations there was also clear evidence that depensatory density-dependent regulation operates on the rate of productivity. Depensation was reported in almost two times the number of studies that reported compensation as a mechanism regulating productivity rates. This positive feedback mechanism on the population size has the potential to be highly destabilising.

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Abbreviations

BAP – British Action Plan

CR – constant recapture probability with time or age class

MR – mark-recapture

OSPAR - The Convention for the Protection of the Marine Environment of the North-East Atlantic

RR – ring-recovery

SD_p – Standard deviation of the demographic process

SE_e – Standard error of the confidence

SMP – Seabird Monitoring Program

VR – variable recapture probability with time or age class

Glossary

Age-class – A group of individuals from the same species that are of similar age. Age-specific demographic parameters are detailed within each species account and accompanying material where possible. The age classes considered in this report are as follows; juvenile (fledging year), immature (years between the fledging year and recruitment), adult (breeding age bird) and senior.

Demographic parameter - A factor that determines the population size. The most important demographic parameters for seabirds and sea ducks are; survival, productivity, recruitment, dispersal and incidence of breeding.

Density-dependence - The influence of population size or density on one or more demographic parameters. This report considers density-dependent regulation acting as either *compensatory* (a negative feedback with population size) or *depensatory* (a positive feedback with population size).

Dispersal – Annual rate of permanent migration from the natal (hatching) or breeding population.

Estimation method – The modelling structure used to estimate recapture rates. This can be constant (CR) or varying (VR) through time. In long-term studies, recovery or re-sighting rates may change (e.g. caused by changes in reporting, protection laws or re-sighting effort). The influence of this process on the estimation of survival will depend on whether the rates were modelled as constant over time or time-dependent.

Family – A scientific taxonomy grouping level, indicating species that typically share similar demographic and ecological traits. The family is detailed for each species in the accompanying material to aid matching of demographic rates between similar species.

Incidence of missed breeding – Annual rate of breeding age birds that do not attempt to breed.

Key Site - The Seabird Monitoring Programme (SMP) has established a UK and Ireland-wide network of four 'Key Site' colonies; Skomer, Canna, Fair Isle and the Isle of May.

Mark-recapture – A technique used to estimate survival rates by re-capturing or re-sighting the identification rings on live birds.

Productivity - The annual population estimate of number of chicks fledged per pair.

Recruitment – The mean age that an individual from a population finishes deferred reproduction and recruits into the breeding population.

Ring-recovery – A technique used to estimate survival rates by recovering of identification ring from dead birds.

Standard deviation of the demographic process – When a demographic parameter is estimated to vary through time either with or without a trend, an estimation of the range is given as the standard deviation of the process (SD_p). For a single study this is the reported standard deviation, and for multiple studies this is the mean of the standard deviations or the standard deviation of the point estimates, whichever is larger.

Standard error of the confidence - When a demographic parameter is estimated to be constant through time, the confidence associated with this point estimate is given as the standard error of the estimate (SE_e).

Survival - The annual population estimate of number of individuals that survive from one breeding season to the next.

1. Introduction

The interaction between seabirds and offshore renewable energy developments has received considerable attention in recent years. Negative consequences include birds colliding with turbines, being displaced from their feeding grounds and wind farms acting as barriers (e.g. Drewitt & Langston 2006; Everaert & Stienen 2007; Johnston *et al* 2014). In order to assess the potential impacts of proposed new developments, population models are used to predict how a population is likely to change following their construction. The type of population model employed has largely depended on the quantity and precision of the demographic data available, and it is currently unclear how many UK seabird and sea duck species have sufficient data to support the development of species specific models.

In some cases, a stochastic Leslie matrix model (Caswell 2001) has been used to assess the potential impacts of offshore renewable developments on seabird and sea duck populations. However, for populations that have been intensively studied, more recent methods have also been used. A limited number of population studies have also included a compensatory density-dependent response (e.g. Freeman *et al* 2014). This negative feedback on population size operates to offset the losses of individuals from the population, for example, a lowered population density may cause a temporary increase in survival or productivity in the remaining individuals, supporting an increase in the population size back towards the long-term average. The use of density-independent population models has generally been considered to be a precautionary approach. However, among certain species, particularly gulls, the influence of density-dependent regulation on demographic rates can also appear as a positive feedback on population size, i.e. it acts as a depensatory mechanism. This mechanism can act to accelerate further population decline and has the potential to be highly destabilising.

This report presents individual species accounts for a selection of British seabirds, sea ducks, divers and grebes. Each account gathers the most up to date published estimates on the following demographic parameters: age-specific survival, age-specific productivity, age of recruitment, incidence of missed breeding, and natal and adult breeding dispersal. Particular attention has been given to regional variation in demographic rates, indicating the extent to which estimates may be applied to other less-well studied colonies. Where possible, the intrinsic and extrinsic factors that influence demographic rates are also detailed. The reported rates should enable population models that assess the impacts of offshore wind farms to be developed as reliably and realistically as possible. Where sufficient data could not be gathered using UK examples, data from colonies outside of the UK have been presented, or a proxy species has been identified. The evidence for density-dependent regulation of seabird demographic rates is also reviewed using examples from the UK, as well as non-UK studies on similar species.

2. Methodology

The project steering group included representatives from the Statutory Nature Conservation Bodies and Marine Scotland Science. The species considered in this report were identified by the Project Steering Group as those most likely to be impacted by offshore renewable developments. An extensive review was conducted for each species of peer-reviewed, scientific literature using the ISI Web of Science database. Grey literature was also explored using the Google Scholar search engine. Each search was conducted using the species scientific name, common name and the demographic terms: survival, productivity OR breeding success, and recruitment. The search was focused on studies from the UK, but when UK information was lacking, the geographic scope was widened. The productivity of several species is monitored annually at four Seabird Monitoring Program (SMP) Key Sites: Canna, Isle of May, Fair Isle and Skomer. Annual reports for the SMP key sites were

obtained from http://jncc.defra.gov.uk/page-4467. For species where insufficient information was obtained through these channels, secondary literature sources were used: Cramp and Simmons (1977, 1983) Cramp (1985) and Baldassarre (2014). Where possible, all relevant articles were obtained in order to extract the relevant information from the text. To facilitate the comparison of demographic studies with different study periods the national population trajectory is detailed for each species. Trends were described based on national census data accessed from http://jncc.defra.gov.uk/page-3201 (JNCC 2014).

2.1. Demographic rates for seabirds in the UK

Survival rates are generally presented as annual estimates. When estimates for more than one colony were identified, the mean was estimated (weighted by the duration of each study) to represent survival across a broader geographic area. Age-specific survival rates are detailed where possible using the following age classes; juvenile (fledging year), immature (years between the fledging year and recruitment in to the breeding population), adult (breeding age bird) and senior. Where immature survival rates have been published as a single value between fledging and recruitment, these rates have not been converted into annual estimates. To construct age-specific models these rates will need to be split into annual rates that reflect the relevant age of recruitment. Caution should be applied when using these estimates to parameterise population models because survival rates of birds typically increase following the first year of life (Caughley 1977). A direct division of the immature survival rate into the recruitment time period is likely to be unrealistic. In the accompanying material, each survival estimate is presented with the methodology used for data collection. This is because the assumptions and biases associated with estimating survival rates from live recapture and dead recovery data differ (see Robinson & Ratcliffe 2010 for review). The biggest difference being that estimates of survival from live recapture models will typically be confounded by permanent emigration (which is equivalent to death within the study, since the individual is no longer available for recapture). This means that survival estimates generated from these models will underestimate the 'true' survival rate by an amount proportional to the degree of dispersal. For breeding adults of some species (e.g. guillemot, puffin) sufficient effort to re-encounter individuals (e.g. Harris *et al* 2000a) will reduce this bias since there is a high degree of site fidelity once individuals recruit to the breeding population. For others species (e.g. Sandwich tern), a high degree of breeding dispersal is likely and this bias may be large (e.g. Ratcliffe *et al* 2008). Each survival estimate in the accompanying material is also presented with the methodology used for estimation. This is because the recovery or re-sighting rates in long-term studies can change with time (e.g. caused by changes in reporting, protection laws or re-sighting effort). The bias on the survival estimates will depend on whether the rates were modelled as constant or varying over time. Estimates modelled using variable recapture rates are likely to be more reliable.

Productivity rates are expressed as the annual population estimate of number of chicks fledged per pair. Where rates of productivity were reported to increase with parental age or experience, annual estimates are also given for each age class separately. Regional trends in productivity rates were assessed using the analysis carried out by Cook and Robinson (2010). A regional mean and variance was estimated by using the grouping highlighted by Cook and Robinson (2010) to categorise the colony-specific rates detailed by Mavor *et al* (2008) and any more recent studies. For species where it was not possible to identify consistent regional trends, but reported large variation between colonies, colony-specific means were presented from Mavor *et al* (2008) and any more recent studies.

The incidence of missed breeding is the proportion of breeding adults that may skip an individual breeding attempt, but continue to breed at the same colony in subsequent years. The rate of breeding dispersal represents the proportion of breeding age individuals that

migrate to breed at other colonies each year, and natal dispersal represents the proportion of individuals in a cohort that recruit into a breeding colony separate from their birth colony. These parameters are given as annual means to illustrate the potential biases associated with the specified estimates of survival and productivity. There is considerably less information available on both of these demographic processes, and they are likely to vary markedly between colonies depending on the local population trend and resource availability. To incorporate these mechanisms into population models would require some degree of qualitative interpretation. Unless specified, recruitment into the breeding population is given as the rounded modal (i.e. most common) value.

All of the demographic parameters identified for each species of seabird and sea duck are detailed in the accompanying material. To assist the accessibility of this information the best available parameters for each species are presented in this report. When a process is estimated to vary temporally either with or without a trend, an estimation of the range is given as the standard deviation of the process (SD_p). For a single study this is the reported standard deviation, and for multiple studies this is the mean of the standard deviations or the standard deviation of the point estimates, whichever is larger. The SD_p of multiple studies will represent the average variability. When a process is estimated to be constant through time, the confidence associated with the point estimate is given as the standard error of the estimate (SE_e). We suggest that, for population modelling purposes, values of $\pm 2*SD_p$ should approximately encompass much of the likely range of variation in each demographic parameter.

Each demographic parameter is presented with a quality and representation score. To assess quality, the estimate is scored on the number of years considered by the study, the number of individuals included per year, and whether an estimation of the range or error is available with the point estimate. Representation is assessed at the national scale; the estimate is scored on whether the data is from the UK, includes recent data (<10 years old), and whether the trajectory of the study colony reflects the current UK population trend. For example, if a study is based on more than 5 years but the population trajectory changed during the study period or does not match the current UK trend, the estimate may receive a good data quality score but a poor representation score (conditional on the other criteria). Each criterion receives a 0 for "no", 1 for "partially/unknown and therefore requiring further evaluation", and 2 for "yes"; scoring quality and representation individually out of 6. The itemisation of the scores for each species is detailed on the second worksheet of the accompanying material.

3.   How to use this report

When interpreting the individual species accounts, it is worth considering that long-term studies and those that include several locations are likely to give more reliable parameter values and be more representative of the inherent variability in these. Estimates based on more than one study are identified in bold in the summary table (Table 33). When selecting values to parameterise population models some qualitative interpretation of the local population trends should also be employed. For species where regionally specific values are recommended in the species account, preference should be given to rates from colonies that have the same population trajectory, as opposed to colonies that are closely distributed.

The assessment of model validity is an essential part of model parameterisation. The model output should be heavily evaluated against the current population trend. If the model does not realistically recreate the local population trend alternative parameter values should be considered. Different modelling frameworks (e.g. stochastic) should also be explored if the quantity and precision of the demographic data available are sufficient.

4. Quality Assurance

An extensive and consistent search of the relevant literature was undertaken by using standardised search terms that were applied to all species. The data in the accompanying material and the body of text presented in this report have been subjected to an internal review by a senior BTO scientist. An earlier version of the report was commented on by the project steering group and all comments were incorporated in the final version. Additional spot-checking between the accompanying material and the report was conducted by Sue O'Brien (JNCC).

5. Species-specific accounts of demographic rates in seabirds

5.1 Sea ducks

5.1.1. Greater scaup (*Aythya marila*)

Table 1. Recommended estimates of demographic rates for the greater scaup.

Demographic parameter	Mean	SD$_p$	SE$_e$	Data quality	Data representation
Age-specific survival					
Juvenile survival (0-1 year) [1]	0.400			3	1
Adult survival [1]	0.810		0.038	5	1
Productivity [1]					
	0.570		0.120	5	1
Age of recruitment [2]					
	2			4	2
Incidence of missed breeding					
	-			-	-
Breeding dispersal					
Natal	-			-	-
Adult	-			-	-

[1]Flint *et al* 2006; [2]Dementiev & Gladkov 1952, cited by Cramp & Simmons 1977.

Recommended demographic rates
Published estimates of survival are largely from breeding populations in North America and Iceland. These include a mark-recapture study (Flint *et al* 2006) and two other studies where the methods were not detailed (Boyd 1962; Austin *et al* 2000). Juvenile survival rates have not been empirically measured but have been estimated based on productivity and population size data (Flint *et al* 2006). At present there are not sufficient data to explore regional variation in survival rates, therefore population models will have to assume the reported estimates of survival to be representative more broadly.

Estimates of local productivity are also limited to a few non-UK studies (see accompanying material greater scaup). Further matching of local population trends is recommended in order to assess the suitability of these estimates for modelling UK birds. At present there are not sufficient data to explore regional variation in productivity rates, and population models will have to assume the reported estimates to be representative more broadly.

Published information on the age of recruitment for greater scaup is relatively old and not based on UK data. Furthermore, the reported estimates differ; recruitment occurs at age 1 (Delacour 1959) or 2 years (Dementiev & Gladkov 1952, cited by Cramp & Simmons 1977). It was not possible to verify the corresponding population trend for these estimates. The older age is presented in Table 1 because it matches the estimates reported for other sea ducks (Tables 1-6). Information on natal and adult dispersal and the incidence of missed breeding is lacking. As a proxy for the incidence of missed breeding it may be appropriate to use estimates based on common eider (Table 2), however further matching of local population trends is recommended in order to assess the suitability of these estimates.

There is large disparity between the rates of breeding dispersal identified for the sea ducks (Tables 1-6). The application of these rates across multiple different species is not recommended.

Population trend in UK
The greater scaup is a UK BAP species and a red-list Bird of Conservation Concern. In the UK they breed in low numbers, but the winter population is supplemented from Iceland, Fennoscandia and Russia (Wernham *et al* 2002). Winter densities are highest in Northern Ireland and Scotland (Kirby *et al* 1993). Numbers in the UK decreased between the late 1980s and early 2010s (Austin *et al* 2014).

Factors influencing survival rates
Populations of greater scaup in Canada are declining and the possible drivers of local survival are reviewed by Austin *et al* (2000).

Factors influencing productivity rates
Populations of scaup in Canada are declining and the possible drivers of local productivity are reviewed by Austin *et al* (2000) and Baldassarre (2014).

Knowledge gaps
The demographic parameters of greater scaup are poorly resolved for the UK and information on the incidence of missed breeding and rates of dispersal are lacking. In the absence of a focused ringing or monitoring program in the UK it will be difficult to improve these estimates based on local data.

5.1.2. Common eider (*Somateria mollissima*)

Table 2. Recommended estimates of demographic rates for the eider.

Demographic parameter	Mean	SD$_p$	SE$_e$	Data quality	Data representation
Age-specific survival					
Juvenile survival (0-1 year) [1]	0.200			2	2
Adult survival ($\geq$2 year) [2-3]	0.886	0.009		6	4
Productivity [4-6]					
	0.379	0.470		5	1
Age of recruitment [1,7]					
	3			3	1
Incidence of missed breeding [2]					
	0.200	0.141		4	2
Breeding dispersal					
Natal	-			-	-
Adult [3]	0.012			4	3

[1]Sperduto *et al* 2003; [2]Coulson 1984; [3]Hario *et al* 2009; [4]Sweenen 1991; [5]Hario & Rintala 2006; [6]Lehikoinen *et al* 2006; [7]Christensen 1999.

Recommended demographic rates
The published estimates of survival for UK common eiders are relatively old (Coulson 1984). There are a number of more recent studies on populations outside of the UK (see accompanying material for common eider), however the local population trends for these studies could not be identified, and further evaluation is needed to assess their suitability for modelling UK eiders. The estimate given for Finland (Hario *et al* 2009) was similar to the UK estimate, and therefore these studies were combined to give the estimate of adult survival in Table 2. At present there are not sufficient data to explore regional variation in survival rates, therefore population models will have to assume the reported estimates to be representative more broadly. Sperduto *et al* (2003) estimated juvenile survival by combining data on similar species. There is some disparity between the estimate of adult survival given by Sperduto *et al* (2003) and the estimate in Table 2. Therefore caution should be applied when using their estimate of juvenile survival to model UK common eider.

Estimates of productivity are also limited to a few non-UK studies that indicate productivity can vary substantially between breeding sites (see accompanying material for common eider). Further matching of local population trends is recommended in order to assess the suitability of these estimates for modelling UK birds.

Eiders are thought to start breeding between the age of 2 and 4 years (Christensen 1999; Sperduto *et al* 2003). It was not possible to verify the corresponding population trend for these estimates; however the mean age is similar to the other estimates reported for sea ducks (Tables 1-6). Outside of the UK, females are thought to remain site faithful once they have recruited (Hario *et al* 2009). Information on natal dispersal is lacking. The incidence of intermittent breeding among eiders was found to increase in relation to population size (Coulson 1984).

Population trend in UK

The density of eiders breeding in the UK is greatest along coastal Scotland and Northern Ireland. During the winter, densities are supplemented by birds of continental origin (Baillie & Milne 1989), and concentrations are highest in south-east Scotland (especially the Firths of Tay and Forth), Cumbria and eastern UK, with smaller numbers also occurring in sheltered locations in western Scotland. Breeding and non-breeding numbers increased markedly during the last century (Kirby *et al* 1993), but more recently, numbers have declined (Austin *et al* 2014).

Factors influencing survival rates

Outside of the UK, adult survival does not show spatial or temporal variation (Alaska, Wilson *et al* 2007). However, large scale mortality events have been linked to the over exploitation of food resources (Camphuysen *et al* 2002), as well as epidemic disease (i.e. avian cholera) (Tjørnløv *et al* 2013).

Factors influencing productivity rates

Productivity increases with age (Baillie & Milne 1982). Local productivity rates have also been linked to winter climate (Lehikoinen *et al* 2006), parent quality, nest location (Bolduc *et al* 2005) and salinity (DeVink *et al* 2005). Productivity rates are also reported to decrease as local population densities increase (Hario & Rintala 2006), and levels of nest predation by gulls increases (Mendenhall & Milne 1985; Mawhinney *et al* 1999; Donehower & Bird 2008). Clutch size has also been negatively linked to population size (Coulson 1999).

Knowledge gaps

Information on breeding dispersal and incidence of missed breeding is lacking. To improve the data quality scores on the age of recruitment and the incidence of missed breeding would require intensive monitoring.

5.1.3. Goldeneye (*Bucephala clangula*)

Table 3. Recommended estimates of demographic rates for the goldeneye.

Demographic parameter	Mean	SD_p	SE_e	Data quality	Data representation
Age-specific survival					
Adult survival [1]	0.770			3	1
Productivity [2]					
	0.365			2	1
Age of recruitment [1-2]					
	3			5	1
Incidence of missed breeding [1-3]					
	Some			-	-
Breeding dispersal					
Natal	-			-	-
Adult [3-5]	0.564	0.125		5	1

[1]Dow & Fredga 1984; [2]Eadie *et al* 1995; [3]Milonoff *et al* 2002; [4]Dow & Fredga 1983; [5]Johnson 1967.

Recommended demographic rates

There are no published estimates of survival for goldeneye in the UK. The estimates of survival published by Dow and Fredga (1984) are based on Swedish breeding populations, and the local population trend could not be identified. Therefore further matching of local population trends is recommended in order to assess the suitability of these estimates for modelling UK goldeneye. At present there are not sufficient data to explore regional variation in survival rates, therefore population models will have to assume the estimate of adult survival from Sweden to be representative more broadly.

Estimates of productivity are lacking because it is difficult to follow chicks after the brood has left the nest site. Chick mortality is highest in the first week following hatching (Paasivaara & Pöysä 2007) and two non-UK studies estimate productivity to 15 days (Milonoff & Paananen 1993; Eadie *et al* 1995). Nest success rates are also reviewed in Baldassarre (2014). Brood survival is low, but it is thought to vary with geographic location and year (Baldassarre 2014). Therefore, colony-specific rates may be more suitable than a national average when parameterising population models for this species. Further matching of local population trends is recommended in order to assess the suitability of the non-UK estimates for modelling UK goldeneye. The values in Table 3 are presented for consideration as national values when parameterising population models for this species.

Published information on the age of recruitment for goldeneye is relatively old and not based on UK data (Dow & Fredga 1984). It was not possible to verify the corresponding population trend for this estimate; however the age is similar to the other estimates reported for sea ducks (Tables 1-6). Some incidence of missed breeding is reported by Dow and Fredga (1984), Eadie *et al* (1995) and Milonoff *et al* (2002), however the rate has not been quantified at the population-level. Breeding dispersal for females is relatively high (Johnson 1967; Dow & Fredga 1983; Eadie *et al* 1995). Furthermore, females that did not breed successfully were more likely to change nesting sites, although distances moved were typically less than 1km (Dow & Fredga 1983). Information on natal dispersal is lacking but thought to be lower for females than males (Dow & Fredga 1983). For the incidence of missed breeding it may be appropriate to use estimates based on eider. Further matching of

local population trends is recommended in order to assess the suitability of these estimates. There is large disparity between the rates of breeding dispersal identified for the sea ducks (Tables 1-6). Therefore the application of these rates across multiple different species is not recommended.

Population trend in UK
A small population of goldeneye breed in Scotland (Musgrove *et al* 2013). Birds winter in both freshwater and coastal habitats, and coastal, winter densities are highest in Scotland (Campbell *et al* 1986). Numbers in the UK declined between 1986 and 2012 (Austin *et al* 2014).

Factors influencing survival rates
The drivers of survival for goldeneye have not been identified.

Factors influencing productivity rates
Outside of the UK, first time breeders have smaller clutches (Dow & Fredga 1984; Milonoff *et al* 2002). Local productivity has been linked to lay date (Dow & Fredga 1984) and availability of nest sites (Pöysä & Pöysä 2002). Productivity rates are reported to be negatively influenced by predation (Andersson & Eriksson 1982; Dow & Fredga 1984), and clutch size (Eriksson 1979), but increase with chick body mass (Paasivaara & Pöysä 2007). There was no evidence for an effect of temperature and rainfall (Paasivaara & Pöysä 2007).

Knowledge gaps
The demographic rates for the UK population of goldeneye are largely unknown. Outside of the UK, productivity and survival rates are also poorly resolved and estimates of breeding dispersal and the incidence of missed breeding are lacking. In the absence of a focused ringing or monitoring program in the UK it will be difficult to improve these estimates based on local data.

5.1.4. Long-tailed duck (*Clangula hyemalis*)

Table 4. Recommended estimates of demographic rates for the long-tailed duck.

Demographic parameter	Mean	SD_p	SE_e	Data quality	Data representation
Age-specific survival					
Adult survival [1-2]	0.730	0.014		5	1
Productivity [3]					
	1.900	0.660		5	1
Age of recruitment [4]					
	2			2	1
Incidence of missed breeding					
	-			-	-
Breeding dispersal					
Natal	-			-	-
Adult	-			-	-

[1]Boyd 1962; [2]Schamber *et al* 2009; [3]Bengtson 1972; [4]Cramp & Simmons 1977.

Recommended demographic rates
In the absence of a focused UK program on long-tailed duck, local survival and productivity rates are largely unknown. Published estimates are from breeding populations in Iceland (survival - Boyd 1962; productivity - Bengtson 1972; see accompanying material for long-tailed duck). The local population trend could not be identified for these studies, and there is no evidence to suggest that the UK population and the Icelandic population overlap on wintering grounds (Wernham *et al* 2002). Estimates based on the other sea duck species may therefore be more appropriate for parameterising population models on this species (Tables 1-6). Further matching of local population trends is recommended in order to assess the suitability of these estimates.

Published information on the age of recruitment for long-tailed duck is relatively old and not based on UK data (Cramp & Simmons 1977). It was not possible to verify the corresponding population trend for this estimate; however the age is similar to the other estimates reported for sea ducks (Tables 1-6). Information on breeding dispersal and the incidence of missed breeding is lacking. The paucity of ring-recoveries and lack of reliable offshore counts means that little is known about site fidelity in this species between winters. As a proxy for the incidence of missed breeding it may be appropriate to use estimates based on eider, however further matching of local population trends is recommended in order to assess the suitability of these estimates. There is large disparity between the rates of breeding dispersal reported for the other sea ducks. Therefore the application of these rates across multiple different species is not recommended.

Population trend in UK
The long-tailed duck is a winter visitor to the UK, breeding in northern Eurasia and North America. Winter densities are highest in the east coast firths of Scotland, but birds also overwinter on Shetland, Orkney and the Outer Hebrides (Campbell *et al* 1986). In the absence of targeted monitoring, exact population trends are unknown (Austin *et al* 2014). Numbers were thought to be relatively stable in the 1980s (Kirby *et al* 1993) but have shown signs of decline in recent decades (Austin *et al* 2014).

Factors influencing survival rates
Mortality in fixed fishing nets can be substantial (Bengtson 1972).

Factors influencing productivity rates
Local productivity rates have been linked to predation (Alison 1975).

Knowledge gaps
Information on age of recruitment, incidence of missed breeding and rates of dispersal are lacking. In the absence of a focused ringing or monitoring program in the UK it will be difficult to improve these estimates based on local data.

5.1.5. Common scoter (*Melanitta nigra*)

Table 5. Recommended estimates of demographic rates for the common scoter.

Demographic parameter	Mean	SD_p	SE_e	Data quality	Data representation
Age-specific survival					
Juvenile survival (0-1 year) [1]	0.749		0.056	3	1
Adult survival [1]	0.783		0.032	3	1
Productivity [2]					
	1.838	1.184		5	1
Age of recruitment [3]					
	3			3	2
Incidence of missed breeding					
	-			-	-
Breeding dispersal					
Natal	-			-	-
Adult	0.123		0.040	4	1

[1]Fox *et al* 2003; [2]Gardarsson and Einarsson 2004; [3]Bengtson 1972; [4]Cramp and Simmons 1977.

Recommended demographic rates
In the absence of a focused UK program on common scoter, local survival and productivity rates are largely unknown. Published estimates are from breeding populations in Iceland (survival - Fox *et al* 2003; productivity - Bengtson 1972; Gardarsson & Einarsson 2004; see accompanying material for common scoter), where a male-biased sex ratio was noted (Bengtson 1972). The local population trend could not be identified for these studies, and consequently the estimates given in Table 5 received low data quality and representation scores. The Icelandic population considered by Bengtson (1972) are likely to overlap with the UK breeding population on wintering grounds (Wernham *et al* 2002), and therefore both populations may experience the same drivers influencing their survival rates. The estimate of juvenile survival appeared very high compared to the rates identified for the other sea duck species (Tables 1-6). Therefore when parameterising population models for common scoter it may be more appropriate to use estimates of juvenile survival from similar species, such as common eider (Table 2).

Published information on the age of recruitment for common scoter is relatively old and not based on UK data (Cramp & Simmons 1977). It was not possible to verify the corresponding population trend for this estimate; however the age is similar to the other estimates reported for sea ducks (Tables 1-6). Female breeding dispersal is thought to be relatively low (Fox *et al* 2003), but information on natal dispersal and the incidence of missed breeding is lacking. As a proxy for the incidence of missed breeding it may be possible to use estimates based on common eider (Table 2), however further matching of local population trends is recommended in order to assess the suitability of these estimates. There is large disparity between the rates of breeding dispersal reported for the other sea ducks (Tables 1-6). Therefore the application of these rates across multiple different species is not recommended.

Population trend in UK
The common scoter is a UK BAP species and a red-list Bird of Conservation Concern. They breed in low numbers in western and northern Scotland (Gibbons *et al* 1993), but the wintering population is inflated with birds that breed in western Siberia and western and northern Europe. Winter densities are highest in coastal areas; the Carmarthen Bay, Liverpool Bay, the Moray and Dornoch Firths and the Firth of Forth (Kirby *et al* 1993). During the 1980s numbers were thought to be relatively stable, although declines were noted in the Moray Firth (Kirby *et al* 1993). More recent trends were not identified.

Factors influencing survival rates
The drivers of survival for common scoter have not been identified.

Factors influencing productivity rates
Outside of the UK, local productivity rates are negatively influenced by decreased food availability, severe weather and avian predation (Cramp & Simmons 1977; Gardarsson & Einarsson 2004).

Knowledge gaps
Information on age of recruitment, incidence of missed breeding and rates of dispersal are lacking for this species. In the absence of a focused ringing or monitoring program in the UK it will be difficult to improve these estimates based on local data.

5.1.6.   Velvet scoter (*Melanitta fusca*)

Table 6. Recommended estimates of demographic rates for the velvet scoter.

Demographic parameter	Mean	SD$_p$	SE$_e$	Data quality	Data representation
Age-specific survival					
Adult survival [1]	0.773		0.018	4	1
Productivity [2]					
	0.350	0.058		3	1
Age of recruitment [3]					
	2			2	2
Incidence of missed breeding					
	-			-	-
Breeding dispersal					
Natal	-			-	-
Adult [4]	0.688			2	1

[1]Krementz *et al* 1997; [2]Traylor *et al* 2004; [3]Hartman *et al* 2013 [4]Brown & Brown 1981.

Recommended demographic rates
In the absence of a focused UK program on velvet scoter, local survival and productivity rates are largely unknown. Published estimates of adult survival are based on similar species (Garthe & Hüppop 2004), or were not published with the methodology used for estimation (Krementz *et al* 1997). Similarly, the majority of published estimates for productivity are relatively old and not based on UK data (Hildén 1964; Waaramaki 1968, cited by Cramp & Simmons 1977; see accompanying material for velvet scoter). The value of productivity given in Table 6 reflects estimates from Canada. Further matching of local population trends is recommended in order to assess the suitability of these estimates for modelling the UK population. The estimates of survival and productivity identified for the other sea duck species should also be considered when parameterising population models for this species (Tables 1-6).

The published estimates for the age of recruitment differ; birds recruit to the breeding population at age 2 (Hartman *et al* 2013) or 3 years (Cramp & Simmons 1977). Both of these values were identified as the modal age for the other sea duck species (Tables 1-6). It was not possible to verify the corresponding population trend for these estimates and therefore the more recent estimate is reported in Table 6. There is some relatively old information on the dispersal of breeding adults from outside of the UK (Brown & Brown 1981). However, information on natal dispersal and the incidence of missed breeding are lacking. As a proxy for the incidence of missed breeding it may be appropriate to use estimates based on common eider (Table 2), however further matching of local population trends is recommended in order to assess suitability.

Population trend in UK
The velvet scoter is a winter visitor to the UK, breeding in Scandinavia and Siberia. Winter densities are highest in the Moray Firth and St Andrews Bay (Kirby *et al* 1993). However, in the absence of targeted monitoring, exact population trends are unknown (Austin *et al* 2014). Regional differences in population change emerged in the 1980s (Kirby *et al* 1993), and signs of decline have been noted in recent decades (Austin *et al* 2014).

Factors influencing survival rates

Survival rates were not related to concentrations of heavy metals (Wayland *et al* 2008), but mortality in fixed fishing nets can be locally substantial (Stempniewicz 1994).

Factors influencing productivity rates

Local productivity rates have been linked to lay dates and brood size (Traylor & Alisauskas 2006). Productivity rates increase during years with favourable weather conditions (Hildén 1964; Traylor & Alisauskas 2006), but decrease in response to predation from mink (Nordström *et al* 2002) and gulls (Finland, Mikola *et al* 1994). Local productivity may also decline at high population densities (Hartman *et al* 2013).

Knowledge gaps

Information on juvenile and immature survival, age of recruitment, incidence of missed breeding and rates of dispersal are lacking. In the absence of a focused ringing or monitoring program in the UK it will be difficult to improve these estimates based on local data.

5.2 Divers

5.2.1. Red-throated diver (*Gavia stellata*)

Table 7. Recommended estimates of demographic rates for the red-throated diver.

Demographic parameter	Mean	SD_p	SE_e	Data quality	Data representation
Age-specific survival					
Juvenile survival (0-1 year) [1]	0.600			2	1
Immature survival (1-2 year) [1]	0.620			2	1
Adult survival (≥3 year) [1-2]	0.840		0.074	4	2
National-average productivity [3-4]					
	0.571	0.222		6	3
Age of recruitment [5]					
	3			4	3
Incidence of missed breeding					
	-			-	-
Breeding dispersal					
Natal	-			-	-
Adult [6]	0.250			2	3

[1]Hemmingsson & Eriksson 2002; [2]Schmutz 2014; [3]Gomersall 1986; [4]Booth 1999; [5]Okill 1994; [6]Okill 1992.

Recommended demographic rates
In the absence of a focused UK ringing program on red-throated diver, there are no published estimates of local survival rate. Outside of the UK, published estimates include a ring-recovery study from Sweden (Hemmingsson & Eriksson 2002) and a mark–recapture study from Alaska (Schmutz 2014). Both of these studies are based on stable populations. The Swedish population considered by Hemmingsson and Eriksson (2002) is likely to overlap with the UK breeding population on wintering grounds (Wernham *et al* 2002). Therefore both populations may experience the same drivers influencing their survival rates. The estimate of adult survival given in Table 7 combined both of these studies and is recommended for modelling stable populations of red-throated diver, such as Shetland and the Hebrides (Dillon *et al* 2009). When constructing population models for populations that are increasing (i.e. Scottish Mainland and the Orkneys) these survival estimates may not be suitable. Regional differences in population trend should be considered when interpreting the outputs of any models parameterised with these values. Juvenile and immature survival rates are poorly resolved due to small sample sizes. Hemmingsson and Eriksson (2002) did not exclude birds ringed as non-fledged chicks, which may cause values to be slightly underestimated. However, the quoted rates appear to be higher than those identified for the black-throated and great northern diver (Table 8; Table 9). These rates should be used with caution in population models, and it may be more suitable to use values estimated for great northern diver (Table 9).

The rate of productivity given in Table 7 is calculated from all the UK estimates listed in the accompanying material for red-throated diver. Although this estimate is derived from relatively old studies where the underlying population trajectory could not be verified, the value is similar to the estimate reported for the stable population breeding in Alaska (Rizzolo *et al* 2014). In the UK, regional differences in population trends have been reported (Dillon *et*

al 2009), but regional trends in productivity have not been investigated (e.g. Cook & Robinson 2010). Colony-specific rates may be more suitable than a national average when constructing population models. These should be selected based on the local population trajectory. For example, the estimates given by Booth (1999) may be more suitable for modelling populations with increasing trends than those given by Gomersall (1986) (see accompanying material for red-throated diver).

Based on a small sample size, birds first breed at age 3 although some may also attempt to breed at age 2 (Okill 1994). This age of recruitment is lower than the estimates identified for black-throated and great northern diver (Table 8; Table 9). Some qualitative interpretation of the local population trends should be employed when parameterising this value in population models, and the age of recruitment reported for black-throated or great northern divers may be more suitable (Table 8; Table 9). In the UK, dispersal of breeding adults is high (Okill 1992), but information on natal dispersal is generally lacking. Hemmingsson and Eriksson (2002) report some fidelity to the natal colony, however small sample sizes prevented reliable estimation of emigration rates.

Population trend in UK
The number of breeding pairs in Orkney and north and west Scotland increased between 1994 and 2006. During the same time period, populations in Shetland and the Hebrides numbers remained relatively stable (Dillon *et al* 2009). Birds overwinter in coastal and near offshore waters around the UK and the population are inflated by individuals from Scandinavia and Greenland (Wernham *et al* 2002). The number of red-throated divers wintering in the UK was relatively stable between the mid-1990s and 2005, but increased between 2005 and 2012 (Austin *et al* 2014).

Factors influencing survival rates
Outside of the UK, local survival rates have been linked to the marine environment, and decrease at high values of the Pacific Decadal Oscillation (i.e. survival rates are lower following warmer sea temperatures and stronger winds, Schmutz 2014).

Factors influencing productivity rates
Outside of the UK, local productivity rates have been linked to flooding risk (Eberl & Picman 1993; Douglas & Reimchen 1988), human disturbance (Rizzolo *et al* 2014) and predation by foxes (Douglas & Reimchen 1988; Rizzolo *et al* 2014).

Knowledge gaps
Adult survival rates for the UK population of red-throated diver are currently unknown, and are poorly resolved for populations outside the UK. Juvenile and immature survival rates are also poorly resolved. There is little information on the incidence of missed breeding and natal dispersal. The estimate for age of recruitment is also based on a small sample size. Further analysis of colour-marking data from Shetland and Orkney may help improve these estimates.

5.2.2. Black-throated diver (*Gavia arctica*)

Table 8. Recommended estimates of demographic rates for the black throated-diver.

Demographic parameter	Mean	SD_p	SE_e	Data quality	Data representation
Age-specific survival					
Juvenile survival (0-1 year) [1]	0.400			2	1
Adult survival (≥2 year) [1-2]	0.817	0.064		4	1
National-average productivity [3-8]					
	0.425	0.292		6	4
Age of recruitment [9]					
	5			3	1
Incidence of missed breeding				-	-
	-			-	-
Breeding dispersal					
Natal	-			-	-
Adult	-			-	-

[1]Hemmingsson & Eriksson 2002; [2]Nilsson 1977; [3]Mudge & Talbot 1993; [4]Hancock 2000; [5]Sharrock 1976; [6]Jackson 2003; [7]Bundy 1979; [8]Thom 1986; [9]Lehtonen 1970.

Recommended demographic rates
In the absence of a focused UK ringing program on black-throated diver, there are no published estimates of local survival rate. The estimates of survival published by Hemmingsson and Eriksson (2002) and Nilsson (1977) are based on Swedish breeding populations. Although the local population trend could not be identified for either of these studies, the wider European and UK breeding populations were both increasing during the 1990s (Hemmingsson & Eriksson 2002; Austin *et al* 2014). The rates of survival estimated by Hemmingsson and Eriksson (2002) are constrained by very small sample sizes; therefore, despite the study being considerably older, the estimate reported by Nilsson (1977) was also included when calculating the estimate of adult survival given in Table 8. Regional variation in the survival rates of black-throated diver has not been investigated. At present there are not sufficient data to model colony-specific survival rates, therefore population models will have to assume that the estimate of adult survival from Sweden is representative more broadly. Juvenile survival rates are poorly resolved due to small sample sizes. Therefore it may be more appropriate to use survival estimates based on the other diver species to build population models for black-throated diver.

Regional trends in population size and productivity rates have not been investigated (e.g. Cook & Robinson 2010). The average rate of productivity given in Table 8 is calculated from all of the UK estimates listed in the accompanying material for black-throated diver. Although these studies are relatively old, the UK population trend is not thought to have changed since the mid-1990s (Austin *et al* 2014). Furthermore, these studies considered large geographic areas and therefore should be representative more broadly.

Published information on the age of recruitment for black-throated diver is also relatively old and not based on UK data (Lehtonen 1970, cited by Nilsson 1977). It was not possible to verify the corresponding population trend for this estimate; however the age is similar to the estimate reported for the great northern diver (Table 9). Hemmingsson and Eriksson (2002)

report some natal and adult site-fidelity, however very small sample sizes (n=3 birds tagged as adults; n=2 birds tagged as chicks) prevented reliable estimation of dispersal rates. The rates of dispersal given for red-throated or great northern diver should be considered when parameterising population models for black-throated diver (Table 7; Table 9). Further matching of local population trends is recommended in order to assess the suitability of these estimates for modelling UK birds.

Population trend in UK
The black-throated diver is a UK BAP species. The European population of black-throated divers increased during the 1990s (Hemmingsson & Eriksson 2002), and this trend has continued in the UK over the last decade (Austin *et al* 2014). More recent trends for outside of the UK could not be identified for this publication.

Factors influencing survival rates
The drivers of survival for black-throated diver have not been identified.

Factors influencing productivity rates
In the UK, local productivity rates have been linked to prey diversity (Jackson 2003, 2005) and floating artificial nesting rafts (Hancock 2000)

Knowledge gaps
The survival rates of black-throated diver in the UK are currently unknown, and are poorly resolved outside of the UK. Information on the incidence of missed breeding and dispersal is lacking, and the age of recruitment is based on relatively old data. In the absence of a focused UK ringing program on black-throated diver it will be difficult to improve these estimates using local data.

5.2.3. Great northern diver (*Gavia immer*)

Table 9. Recommended estimates of demographic rates for the great northern diver.

Demographic parameter	Mean	SD$_p$	SE$_e$	Data quality	Data representation
Age-specific survival					
Immature survival (0-3 year) [1]	0.770		0.020	6	2
Adult survival (≥4 year) [1-2]	0.870		0.078	6	2
Productivity [3-6]					
	0.543	0.170		6	1
Age of recruitment [7]					
	6			3	1
Incidence of missed breeding [7]					
	0.307			3	1
Breeding dispersal					
Natal [1]	0.069			2	2
Adult [2]	0.090	0.166		6	1

[1]Piper *et al* 2012; [2]Mitro *et al* 2008; [3]Belant & Anderson 1991; [4]Croskery 1991; [5]Timmermans *et al* 2005; [6]Grear *et al* 2009; [7]Evers 2004.

Recommended demographic rates
The great northern diver is a winter visitor to the UK that breeds in Iceland. In the absence of a focused ringing program in Iceland, the local survival rates are largely unknown. Published estimates are limited to breeding populations in New England and Wisconsin; including a ring-recovery (Mitro *et al* 2008) and two mark–recapture studies (Mitro *et al* 2008; Piper *et al* 2012). These studies identified drivers of survival that were similar to those identified to influence the productivity of black-throated diver in the UK; e.g. fluctuating water levels (UK – Hancock 2000; US – Piper *et al* 2002) and water chemistry (UK – Jackson 2005; US – Piper *et al* 2012). The estimates of survival in Table 9 appear to be higher than those identified for the other two species of diver. However, the higher data quality score attained by these studies indicates that they are likely to be more robust. The rates for juvenile and immature survival given by Piper *et al* (2012) are adjusted for natal dispersal and therefore the bias on true survival rate may be low. In America, adult survival rates are similar across different regions (Mitro *et al* 2008). Therefore, these rates may be suitable for modelling the population of great northern divers that winter in the UK.

There is little published information on the productivity of great northern divers breeding in Iceland. Therefore the rate of productivity given in Table 9 reflects estimates from America and Canada (see accompanying material for great northern diver). One of the identified drivers of productivity in America and Canada is similar to that identified to influence black-throated diver breeding in the UK; water chemistry (UK – Jackson 2005; US – Piper *et al* 2012). Therefore this value may be suitable for modelling the productivity of UK birds.

The mean age of first breeding is higher than identified for the other two species of diver considered (range 4-11 years; Evers *et al* 2000, cited by Evers 2004). In America, adult and natal breeding dispersal is thought to be low (Mitro *et al* 2008; Piper *et al* 2012), and the incidence of missed breeding is thought to be high (Yonge 1981, cited by Evers 2004; Taylor & Vogel 2003, cited by Evers 2004).

Population trend in UK
The wintering population increased during the late 1990s, but stabilised between 2000 and 2012 (Austin *et al* 2014).

Factors influencing survival rates
Outside of the UK, local survival rates have been linked to water chemistry and lake size (Piper *et al* 2012), nest location and mercury levels (Mitro *et al* 2008). In America, survival rates do not appear to differ between the sexes (Mitro *et al* 2008).

Factors influencing productivity rates
Outside of the UK, local productivity rates have been linked to water chemistry, lake-size (Piper *et al* 2012) and population size (Evers 2004).

Knowledge gaps
The demography of great northern divers wintering in the UK is poorly resolved. In the absence of a focused ringing or monitoring program in Iceland it will be difficult to improve these estimates based on local data.

5.3 Procellariiformes

5.3.1. Manx shearwater (*Puffinus puffinus*)

Table 10. Recommended estimates of demographic rates for the Manx shearwater.

Demographic parameter	Mean	SD$_p$	SE$_e$	Data quality	Data representation
Age-specific survival					
Adult survival [1]	0.870	0.080		6	4
Experience-specific productivity					
1st attempt [2]	0.630	0.141		2	3
>1 attempt [2]	0.781	0.118		2	3
Colony-specific productivity					
Rum [3]	0.680	1.442		6	4
Sanda [3]	0.890	0.134		6	4
Skomer [1]	0.598	0.098		6	4
Bardsey [3]	0.810	0.032		6	4
National-average productivity [1,3]					
	0.697	0.426		6	4
Age of recruitment [4]					
	5			2	3
Incidence of missed breeding [5]					
	0.157			2	3
Breeding dispersal					
Natal [6-7]	Low			-	-
Adult [4]	Low			-	-

[1]Büche *et al* 2013; [2]Brooke 1978a; [3]Mavor *et al* 2008; [4]Harris 1966; [5]Perrins *et al* 1973; [6]Harris 1972; [7]Brooke 1978b.

Recommended demographic rates
The UK estimates of survival for Manx shearwater are largely limited to Wales (see accompanying material for Manx shearwater). They include a relatively old ring-recovery and mark-recapture study from Skokholm that adjusted the estimates of survival for the occurrence of skipped breeding (Perrins *et al* 1973). Therefore the bias on true survival rate may be low. More recent estimates include a mark-recapture analysis from Skomer (Büche *et al* 2013; Table 10). Regional variation in survival rates has not been investigated; therefore population models will have to assume the estimates of adult survival from Wales to be representative more broadly. Juvenile and immature survival rates are more difficult to resolve due to lower recovery rates. In Perrins *et al* (1973), the sample of years and individuals was too small for reliable conclusions to be drawn. More recent attempts to estimate survival during this life stage have not been made.

Regional trends in productivity have not been investigated for this species (e.g. Cook & Robinson 2010). Consequently, it may be more suitable to use colony-specific rates of

productivity to parameterise population models on this species (Table 10). The productivity of Manx shearwater is monitored annually at one SMP Key Site: Skomer, and long-term productivity estimates are given for three additional UK localities by Mavor *et al* (2008).

The age of first breeding has been explored by aging Manx shearwaters ringed as young and later found with an egg (Harris 1966). The modal age was 5 years, however a large proportion were also 6 or 7 years old at first breeding. Because some of the older birds in this study might have bred one or more seasons before being discovered, these results cannot be taken as definite ages of first breeding. Harris (1966) also reports that the modal age of first return following deferred reproduction occurs at 4 years old. Given that seabirds often prospect breeding sites during the year of first return, a modal age of first breeding at 5 years appears to be sensible. Local incidence of missed breeding has been estimated on Skokholm (Perrins *et al* 1973), but this study is based on one year and is therefore unlikely to be representative more widely. Breeding dispersal of adult Manx shearwaters is low and any movements within a colony are usually short (Harris 1966; Perrins *et al* 1973). Natal dispersal also appears to be low (Skokholm, Harris 1972), especially for males (Skokholm, Brooke 1978b).

Population trend in UK
Manx shearwaters breed exclusively on islands, and of the UK population, 40% breed on Rum, and 50% in Pembrokeshire on the adjacent islands of Skomer, Skokholm and Middleholm. Exact population trends are difficult to verify because of the nocturnal and subterranean habit of this species (JNCC 2014).

Factors influencing survival rates
The drivers of survival for Manx shearwater have not been identified.

Factors influencing productivity rates
There is no evidence that local productivity rates are influenced by rainfall flooding burrows (Thompson & Furness 1991). On Skokholm, productivity of first time breeders was relatively low, stabilising from the second attempt (Brooke 1978a).

Knowledge gaps
Existing ring-recovery and sighting data should be sufficient to estimate adult survival rates away from Wales and investigate regional trends. Other active mark-recapture studies are on Rum and Copeland. There is little information on juvenile and immature survival rates, and breeding dispersal rates have not been quantified. Assuming low levels of natal dispersal, one approach would be to solve for juvenile survival based on other demographic parameters and population trend data from a regularly monitored site (e.g. Skomer). To improve the data quality scores on the incidence of missed breeding and the age of recruitment would require intensive monitoring.

5.3.2. Northern fulmar (*Fulmarus glacialis*)

Table 11. Recommended estimates of demographic rates for the northern fulmar.

Demographic parameter	Mean	SD$_p$	SE$_e$	Data quality	Data representation
Age-specific survival					
Immature survival (0-8 years)[1]	0.260	0.150		6	1
Adult survival [2]	0.936	0.055		6	3
Colony specific productivity					
Ailsa Craig [3]	0.740	0.112		6	3
Handa [3]	0.460	0.124		6	3
St. Kilda [3]	0.280	0.072		6	3
Canna [3]	0.400	0.089		6	3
Hermaness [3]	0.410	0.124		6	3
Burravoe [3]	0.320	0.017		4	3
Eshaness [3]	0.420	0.089		6	3
Noss [3]	0.400	0.108		6	3
Foula [3]	0.390	0.000		4	3
Troswick Ness [3]	0.390	0.089		6	3
Sumburgh Head [3]	0.450	0.089		6	3
Fair Isle [4]	0.426	0.087		6	4
North Ronaldsay [3]	0.230	0.170		6	3
Papa Westray [3]	0.480	0.190		6	3
Rousay [3]	0.520	0.150		6	3
Eynhallow [5]	0.414	0.138		6	3
Costa Head [3]	0.470	0.124		6	3
Mull Head [3]	0.400	0.124		6	3
Gultak [3]	0.400	0.124		6	3
Old Man, Hoy [3]	0.450	0.133		6	3
Wilkhaven [3]	0.220	0.210		6	3
Easter Ross [3]	0.160	0.139		6	3
Isle of May [6]	0.346	0.101		6	4
Tantallon [3]	0.310	0.218		6	3
Farne Islands [3]	0.540	0.089		6	3
Coquet Island [3]	0.460	0.150		6	3
Marsden Cliffs [3]	0.230	-		4	3
Peel Headlands [3]	0.340	0.246		6	3
Glen Maye [3]	0.350	0.174		6	3
Bardsey [3]	0.740	0.112		6	3
Skomer [7]	0.327	0.131		6	4
National-average productivity [3-7]					
	0.419	0.127		6	4

Demographic parameter	Mean	SD_p	SE_e	Data quality	Data representation
Age of recruitment [8]					
	9			4	3
Incidence of missed breeding					
	-			-	-
Breeding dispersal					
Natal [9]	0.915	0.035		5	3
Adult [10-11]	Low			-	-

[1]Jenouvrier *et al* 2003; [2]Grosbois & Thompson 2005; [3]Mavor *et al* 2008; [4]Shaw *et al* 2010; [5]Lewis *et al* 2009; [6]Newell *et al* 2010; [7]Büche *et al* 2013; [8]Ollason & Dunnet 1978b; [9]Dunnet *et al* 1979; [10]Macdonald 1977; [11]Hatch 1987.

Recommended demographic rates
The UK estimates of survival for northern fulmar are largely limited to Eynhallow, Orkney (see accompanying material for northern fulmar). They include two mark-recapture studies, conducted almost 30-years apart, that report similar estimates of adult survival (Dunnet & Ollason 1978a; Grosbois & Thompson 2005). The estimate of adult survival given in Table 11 reflects the more recent study that utilises a longer time series (Grosbois & Thompson 2005). Juvenile and immature survival rates are more difficult to resolve because few rings are recovered for these age-classes. As a proxy for survival between fledging and first return to the colony, it may be appropriate to use estimates based on southern fulmars (Jenouvrier *et al* 2003). Converted into an annual rate of survival (using the age of recruitment for southern petrel, 11±4 years, Jenouvrier *et al* 2003), the quoted rates for immature survival appear to be higher than the rates identified for the other species of seabird considered in this report (0.884). Therefore it may be more suitable to use juvenile survival estimates from other Procellariiform species. Regional variation in survival rates has not been investigated; however regional differences in population trends could not be wholly attributed to local differences in breeding success (Cook & Robinson 2010). At present there are not sufficient data to model colony-specific survival rates for northern fulmar, therefore population models will have to assume the estimates from Orkney are representative more broadly. It will be important to consider the regional differences in population trend as caveats of population models that are developed for colonies away from Orkney.

Cook and Robinson (2010) could not identify consistent trends in the productivity of northern fulmar within the SMP and OSPAR regions. Consequently, it may be more suitable to use colony-specific rates of productivity to parameterise population models on this species (Table 11). The productivity of northern fulmars is monitored annually at all four SMP Key Sites: Isle of May, Canna, Fair Isle and Skomer, and long-term productivity estimates are given for 27 additional UK localities by Mavor *et al* (2008).

Published information on the age of recruitment for northern fulmar is relatively old (Ollason & Dunnet 1978), and national census data indicate that the trajectory of the UK population has changed since this study; from increasing to decreasing (Austin *et al* 2014). Therefore caution should be applied when using the reported age to model current population trends (Table 11). The reported age is considerably higher than reported for other UK seabirds, but is similar to the closely related southern fulmar (11±4 years, Jenouvrier *et al* 2003). Consequently, the difference to the other seabirds may reflect life history strategy, as opposed to population trajectory. Some missed breeding is reported by Carrick (1954) and Ollason and Dunnet (1983), however small sample sizes prevented population rates being reliably quantified. Some tendency for individuals to skip breeding in response to environmental factors is reported for southern (Jenouvrier *et al* 2003) and northern fulmars

(Thompson & Ollason 2001). In the UK, the proposed mechanism is lower recruitment of sand eels during the previous winter (Thompson & Ollason 2001). Adult dispersal has not been quantified, but very high mate and site-fidelity indicates that this parameter is likely to be low (MacDonald 1977; Hatch 1987). In contrast, natal breeding dispersal is thought to be extremely high (Dunnet *et al* 1979). Although this estimate comes from a relatively old study, high levels of natal dispersal will strongly influence the subsequent population trajectory. This process requires consideration when building population models for this species.

Population trend in UK
The northern fulmar breeds throughout the British coastline, and national census data indicate that UK colonies rapidly increased between 1969 and 1998, stabilised between the late 1980s and early 2000s, and declined between 2000 and 2013 (JNCC 2014). The recent decline was attributed in part to a decline in discards from trawler fisheries. Regional differences in the rate of decline were identified in three discrete geographic areas; one surrounding the Irish Sea, one on the West coast of Scotland and one covering Orkney, Shetland and the East Coast of Scotland and Northern England (Cook & Robinson 2010).

Factors influencing survival rates
Local survival has been linked to the marine environment, and decrease at high values of the winter Northern Atlantic Oscillation (i.e. survival rates are lower following warmer sea temperatures and stronger winds, Grosbois & Thompson 2005). Survival does not appear to differ between the sexes (Dunnet & Ollason 1978a).

Factors influencing productivity rates
Local productivity rates have been linked to parental age and quality (Dunnet & Ollason 1978b; Ollason & Dunnet 1978; Lewis *et al* 2009), as well as lay dates (Hatch 1990). Productivity rates are also reported to be negatively influenced by a decrease in prey biomass (Grey *et al* 2003), and also decrease at high values of the winter Northern Atlantic Oscillation (i.e. productivity rates are lower following warmer sea temperatures and stronger winds, Thompson & Ollason 2001; Lewis *et al* 2009). There is no evidence that productivity depends on nesting density (Lewis *et al* 2009).

Knowledge gaps
Juvenile and immature survival rates are largely unknown, and high levels of natal dispersal will make this parameter difficult to deduce without multi-colony studies. However, this would also permit adult breeding dispersal to be quantified. The reported age of recruitment reflects a period when the population trajectory differed from the present day, and the incidence of missed breeding is not resolved. These parameters could potentially be examined using the long-term monitoring data from Orkney.

5.4 Gannet

5.4.1. Northern gannet (*Morus bassanus*)

Table 12. Recommended estimates of demographic rates for the northern gannet.

Demographic parameter	Mean	SD_p	SE_e	Data quality	Data representation
Age-specific survival					
Juvenile survival (0-1 year) [1]	0.424		0.007	6	3
Immature survival (1-2 years) [1]	0.829		0.004	6	3
Immature survival (2-3 years) [1]	0.891		0.003	6	3
Immature survival (3-4 years) [1]	0.895		0.003	6	3
Adult survival ($\geq$5 year) [1]	0.919	0.042		6	3
Experience-specific productivity					
1st attempt [2]	0.553		0.019	3	3
2nd attempt [2]	0.645			1	3
3rd attempt [2]	0.770			1	3
$\geq$4th attempt [2]	0.817			1	3
Regional-specific productivity					
East [1-5]	0.698	0.071		6	4
West [3-4]	0.710	0.105		6	4
National-average productivity [1-3, 5]					
	0.700	0.082		6	4
Age of recruitment [1-2]					
	5			5	3
Incidence of missed breeding					
	-			-	-
Breeding dispersal					
Natal	-			-	-
Adult [6]	Low			-	-

[1]Wanless *et al* 2006; [2]Nelson 1966; [3]Mavor *et al* 2008; [4]Cook & Robinson 2010; [5]Shaw 2010; [6]Nelson 1965.

Recommended demographic rates
The survival rates of northern gannet in the UK are relatively well resolved and recent estimates include a ring-recovery analysis that considers regional differences in survival (see accompanying material for northern gannet). The identified differences were attributed to the relatively low number of individuals ringed as adults at colonies other than Bass Rock (Wanless *et al* 2006). Furthermore, regional differences in population trends were largely attributed to local differences in breeding success (Cook & Robinson 2010). Therefore, it may be sufficient to employ a national average for survival when parameterising population models for this species. The study by Wanless *et al* (2006) examined ten colonies in the UK and excluded ring-recoveries of birds found dead or recaptured alive at the colony. Therefore, the estimates of survival given in Table 12 are unlikely to be biased by natal or adult dispersal.

Regional trends in productivity rates were identified in two discrete geographic areas (Cook & Robinson 2010; Appendix S1 for map). The productivity of northern gannets is monitored annually at one SMP Key Site: Fair Isle, and long-term productivity is given for seven additional UK localities by Nelson (1966), Wanless *et al* (2006), Mavor *et al* (2008) and Shaw *et al* (2010) (see accompanying material for northern gannet). The range of productivity values given in Table 12 were calculated using the regional groupings highlighted by Cook and Robinson (2010) to categorise the values specified by Nelson (1966), Wanless *et al* (2006), Mavor *et al* (2008) and Shaw *et al* (2010). The published information on experience-specific productivity rates is relatively old (Table 12). These values should be used in population models to guide the proportional change that can be expected with age, as opposed to absolute values of productivity.

Published information on the modal age of recruitment for northern gannet is available from two studies conducted 40 years apart (Nelson 1966; Wanless *et al* 2006). Although the rate of population growth has changed during this time (Wanless *et al* 2006; Murray *et al* 2006; JNCC 2014), the reported age of recruitment was similar in both studies (Table 12). Adult breeding dispersal is thought to be low (Nelson 1965) but has not been quantified at the population level. Information on natal breeding dispersal and the incidence of missed breeding is also lacking. It may be necessary to identify proxy species from outside of the UK to parameterise these processes in population models.

Population trend in UK
There are 21 gannet colonies around the British Isles, and the majority of these occur on remote offshore islands and stacks, with two on mainland cliffs. National census data indicate that the majority of colonies in the UK increased rapidly between 1969 and 2002 (JNCC 2014). More recently, this rate of increase is thought to have slowed (Wanless *et al* 2006; Murray *et al* 2006). The rate of increase varies consistently within two discrete geographic areas; the first covering Orkney, the West Coast of the United Kingdom and Ireland and the second covering Shetland and the East Coast of the United Kingdom (Cook & Robinson 2010).

Factors influencing survival rates
The drivers of survival for northern gannet have not been identified.

Factors influencing productivity rates
Local productivity rates have been linked to parental experience and increase sequentially between the first and the fourth breeding attempt (Nelson 1966).

Knowledge gaps
The juvenile and immature survival rates for northern gannets are poorly resolved, and breeding dispersal and the incidence of non-breeding are largely unknown. The incidence of missed breeding could potentially be explored using long-term monitoring data from Fair Isle, however the estimation of other demographic parameters would require intensive monitoring and multi-colony studies. Assuming that natal dispersal is low, an alternative approach would be to solve for juvenile survival rates based on other demographic parameters and population trend data collected from a regularly monitored site (e.g. Isle of May).

5.5 Grebe

5.5.1. Great crested grebe (*Podiceps cristatus*)

Table 13. Recommended estimates of demographic rates for the great crested grebe.

Demographic parameter	Mean	SD$_p$	SE$_e$	Data quality	Data representation
Age-specific survival					
Adult survival (>4 years) [1-2]	0.725		0.028	4	2
Productivity [1,3]					
	1.275	0.035		4	3
Age of recruitment [1,4]					
	2			2	3
Incidence of missed breeding					
	-			-	-
Breeding dispersal					
Natal	-			-	-
Adult	-			-	-

[1]Abt & Konter 2009; [2]Fuchs 1982; [3]Prestt & Jefferies 1969; [4]Cramp & Simmons 1977.

Recommended demographic rates
There are no published estimates of survival for the great crested grebe in the UK. Published estimates of adult survival include two ring-recovery studies that examine data collected across extensive areas (Germany, Fuchs 1982, cited by Garthe & Hüppop 2004; and Europe, Abt & Konter 2009). Further matching of local population trends is recommended in order to assess the suitability of these estimates for modelling the UK population. At present there are not sufficient data to model colony-specific survival rates, therefore population models will have to assume that these estimates are representative more broadly. The estimate of immature survival reported by Abt and Konter (2009) is not listed in Table 13 because it extends past the age of recruitment (see accompanying material for great crested grebe). It may be necessary to identify proxy species to parameterise the survival rates of great crested grebe in population models.

Estimates of productivity are also limited to a few studies (see accompanying material for great crested grebe). These include an old estimate for the UK (Prestt & Jefferies 1969) and a more recent estimate for Europe (Abt & Konter 2009). Further matching of local population trends is recommended in order to assess the suitability of these estimates for modelling UK birds. A limited proportion of great crested grebes can also successfully fledge two broods within one breeding season (4.3%, Harrison & Hollom 1932; 4.6%, Simmons 1974). This mechanism should be considered when constructing population models for this species.

The age of first breeding is thought to occur at age 2 (Abt & Konter 2009; Cramp & Simmons 1977), although birds may pair and hold territory from their first year (Cramp & Simmons 1977). Information on natal and adult dispersal and the incidence of missed breeding is lacking. Consequently, it may be more appropriate to use estimates based on the diver species to parameterise these processes in population models. Further matching of local population trends and demographic processes is recommended in order to assess the suitability of other species for modelling great crested grebe.

Population trend in UK
In the UK, the great crested grebe is widely, although thinly distributed. They breed on large, shallow inland waters, and some move to coastal waters during winter. The UK population declined between 2002 and 2012 (Austin *et al* 2014).

Survival rates
The drivers of survival for great crested grebe have not been identified.

Productivity rates
Outside of the UK, local productivity rates are reported to be positively influenced by increased prey availability (Ulenaers & Dhont 1994; Ulfvens 1988), but are negatively influenced by predation levels associated with human disturbance (Keller 1989).

Knowledge gaps
Juvenile and immature survival rates are poorly resolved. Information on natal and adult dispersal, as well as missed breeding is also lacking. In the absence of a focused ringing or monitoring program in the UK it will be difficult to improve these estimates based on local data.

5.6 Cormorants

5.6.1 Great cormorant (*Phalacrocorax carbo*)

Table 14. Recommended estimates of demographic rates for the great cormorant.

Demographic parameter	Mean	SD_p	SE_e	Data quality	Data representation
Age-specific survival					
Juvenile survival (0-1 year) [1-2]	0.540		0.090	6	1
Adult survival (>3 year) [1-2]	0.868	0.055		6	1
Experience-specific productivity					
1st attempt [3]	1.445			4	1
2nd attempt [3]	1.758			4	1
3rd attempt [3]	2.076			4	1
≥4th attempt [3]	2.274			4	1
Regional-specific productivity					
An Glas Eilean [4]	1.730	1.010		6	4
North Sutor [4]	2.060	0.581		6	4
Ballard Cliff [4]	1.340	0.201		6	4
Ynysoedd Gwylan [4]	2.970	0.759		6	4
Skomer [4]	1.590	0.710		6	4
South Solway "B" [4]	1.090	0.980		4	4
Will's Strand [4]	2.480	0.106		6	4
Caithness [4]	2.652	0.752		4	4
National-average productivity [4-5]					
	1.985	0.666		6	4
Age of recruitment [6-7]					
	3			5	1
Incidence of missed breeding					
	-			-	-
Breeding dispersal					
Natal [1-2]	0.240	0.127		6	1
Adult [2,7]	0.123	0.042		6	1

[1]Frederiksen & Bregnballe 2000a; [2]Hénaux *et al* 2007; [3]Bregnballe 2006; [4]Mavor *et al* 2008; [5]Budworth *et al* 2000; [6]Kortlandt 1942; [7]Frederiksen & Bregnballe 2000b.

Recommended demographic rates
The UK estimates of adult survival for *P. carbo* are relatively old and based on ring-recovery studies from Caithness, NE Scotland (Wernham & Peach 1999; Budworth *et al* 2000). The reported values are considerably lower than those identified for the other seabird species, possibly due to hunting activities changing levels of survival and emigration (Wernham & Peach 1999; see accompanying material for great cormorant). The breeding biology of *P. carbo* and *P. c. sinensis* (the continental race) is highly similar; therefore demographic rates

may be interchangeable for these populations. The values of adult survival given in Table 14 are estimated from mark-recapture studies on the continental race (Frederiksen & Bregnballe 2000a; Hénaux *et al* 2007). In the UK, regional differences in population trends could not be wholly attributed to local differences in breeding success (Cook & Robinson 2010). However, at present there are not sufficient data to model colony-specific survival rates. It will be important to consider these regional differences in population trend as caveats of any population models developed. Furthermore, *P. c. sinensis* has increased rapidly in recent decades (Frederiksen & Bregnballe 2000a), and local population trajectories should be matched before extrapolating these rates across multiple colonies.

Cook and Robinson (2010) could not identify regional trends in the productivity of cormorants within the SMP and OSPAR regions. Consequently, it may be more suitable to use colony-specific rates of productivity to parameterise population models on this species (Table 14). The productivity of great cormorant (*P. carbo*) is monitored annually at one SMP Key Site: Skomer, and long-term productivity is given for six additional UK localities by Mavor *et al* (2008). Published information on experience-dependent productivity for great cormorant is not from the UK (Table 14; Bregnballe 2006). These values should be used in population models to guide the proportional change that can be expected with age, as opposed to absolute values of productivity.

The majority of birds breed for the first time at age 3 (range 2-5, *P. c. sinensis* - Kortlandt 1942; Frederiksen & Bregnballe 2000b). Although Budworth *et al* (2000) provide some information on inter-colony movements of *P. carbo* in Scotland, information on natal and adult dispersal is largely lacking for the UK. The natal and adult dispersal rates detailed in Table 14 are for the continental race (Frederiksen & Bregnballe 2000a; Hénaux *et al* 2007). Information on the incidence of missed breeding is lacking.

Population trend in UK
National census data indicate that great cormorant populations increased slightly between the 1970s and 2000, but have declined between 2000 and 2013 (JNCC 2014). Regional differences in population trends were identified in seven discrete geographic areas; Shetland, Orkney and North Scotland, East Scotland, East England, South East England, South and West England and East Ireland and West Scotland. Colonies in Orkney, North Scotland, East Ireland and West Scotland were declining, whilst the others were increasing (Cook & Robinson 2010). Furthermore, there is an increasing number of the continental race *P. c. sinensis* now overwintering in the UK (Newson *et al* 2005).

Factors influencing survival rates
Local survival rates of *P. c. sinensis* decrease when winter sea temperatures increase and this effect is greater at high population densities (Frederiksen & Bregnballe 2000a). Survival rates do not appear to differ between the sexes (Frederiksen & Bregnballe 2000a).

Factors influencing productivity rates
Local productivity is higher at inland colonies compared to coastal colonies (Newson *et al* 2005). Outside of the UK, local productivity rates of *P. c. sinensis* have been linked to concentrations of contaminants (Dirksen 1995), and in Denmark, productivity increases with parental experience up the fourth breeding attempt (Bregnballe 2006).

Knowledge gaps
There is a large quantity of data on colour-ringed cormorants that could be used to assess regional differences in survival. To resolve the incidence of missed breeding would require intensive monitoring of a marked population.

5.6.2 European shag (*Phalacrocorax aristotelis*)

Table 15. Recommended estimates of demographic rates for the European shag.

Demographic parameter	Mean	SD$_p$	SE$_e$	Data quality	Data representation
Age-specific survival					
Juvenile survival (0-1 year) [1]	0.513	0.246		6	4
Immature survival (1-2 year) [1]	0.737	0.181		6	4
Adult survival ($\geq$3 year) [1]	0.858	0.194		6	4
Age-specific productivity					
1st attempt [2]	0.532	0.049		3	4
$\geq$2nd attempt [2]	0.785	0.042		3	4
Regional-specific productivity					
West [3-4]	2.135	0.322		6	4
North [3-4]	1.277	0.456		6	4
East [3-5]	1.132	0.511		6	5
National-average productivity [3,5]					
	1.303	0.483		6	5
Age of recruitment [6]					
	2			4	2
Incidence of missed breeding					
	-			-	-
Breeding dispersal					
Natal [7]	0.049			2	2
Adult [8]	0.100			4	5

[1]Frederiksen *et al* 2008; [2]Daunt *et al* 1999; [3]Mavor *et al* 2008; [4]Cook & Robinson 2010; [5]Newell *et al* 2010; [6]Aebischer 1986; [7]Aebischer 1995; [8]Barlow *et al* 2013.

Recommended demographic rates

The UK estimates of survival for European shag are largely limited to the Isle of May, SE Scotland (see accompanying material for European shag). There is also a relatively old ring-recovery study from the Farne Islands, NE England (Coulson & White 1957). The rates reported from this older study were considerably lower than those reported from the Isle of May using mark-capture analysis. This is most likely due to the old-style rings becoming worn and illegible with time (Coulson & White 1957), and therefore these estimates are likely to be unreliable. The estimates of adult survival from the Isle of May were largely similar. The survival rates detailed in Table 15 are taken from Frederiksen *et al* (2008) because the time series considered spanned most of the other studies. Regional differences in population trends could be largely attributed to local differences in breeding success (Cook & Robinson 2010). Therefore, it may be sufficient to assume that the Isle of May estimate of survival are representative more broadly.

Regional trends in productivity rates were identified in three discrete geographic areas (Cook & Robinson 2010; Appendix S2 for map). The productivity of the European shag is

monitored annually at three SMP Key Sites: Isle of May, Canna and Skomer, and long-term productivity estimates are given for 18 additional UK localities by Mavor *et al* (2008). The range of productivity values given in Table 15 were calculated using the regional groupings highlighted by Cook and Robinson (2010) to categorise the values specified by Mavor *et al* (2008) and Newell *et al* (2010). These estimates indicate large variability to occur within each region. Published information on experience-dependent productivity for European shag is relatively old (Table 15; Daunt *et al* 1999). These values should be used in population models to guide the proportional change that can be expected with age, as opposed to absolute values of productivity.

Published information on the age of recruitment for the European shag is relatively old. The European shag typically breeds for the first time at age 2, although individuals may also defer breeding until they are 3 or 4 years old (Aebischer 1986). National census data indicate that the trajectory of the UK population has changed since this estimate was published; from increasing to decreasing (JNCC 2014). Caution should be applied when using the reported age to model current population trends (Table 15). Adult breeding dispersal is thought to be low (Barlow *et al* 2013). Similarly, natal dispersal is also thought to be low, but may vary between colonies (Aebischer 1995). Information on the incidence of missed breeding is lacking. It may be appropriate to substitute this parameter with estimates from great cormorant (Table 14), although further matching of population trends is recommended.

Population trend in UK
The European shag is distributed throughout UK coastal waters. National census data indicate that the majority of colonies in the UK increased between 1969 and 1988, but numbers declined between the late 1980s and 2012 (JNCC 2014). The rate of decline varies within four discrete geographic areas; the first covering the West Coast of Scotland, the second covering the West Coast of England and Wales, the third covering the East Coast of Scotland and Orkney and the fourth covering Shetland (Cook & Robinson 2010).

Factors influencing survival rates
Decreased levels of survival have been linked to toxic poisoning (Coulson *et al* 1968), as well as offshore winds and rainfall (Frederiksen *et al* 2008).

Factors influencing productivity rates
Initially, productivity rates depend on parental age and quality (Daunt *et al* 1999). However, after the first attempt there is no evidence that productivity depends on age, nest density, pair status, and site or mate fidelity (Potts *et al* 1980). Large-scale non-breeding events have been associated with poor feeding conditions (Aebischer & Wanless 1992).

Knowledge gaps
The age of recruitment was estimated during a period where the population trajectory differed from the present day. Information on the average incidence of missed breeding is also lacking. Estimation of these demographic parameters could potentially be achieved using the long-term monitoring data from the Isle of May. There is also a large quantity of mark-recapture data collected as part of the British and Irish ringing scheme that could provide estimates of regional survival.

5.7. Skuas

5.7.1. Arctic skua (*Stercorarius parasiticus*)

Table 16. Recommended estimates of demographic rates for Arctic skua.

Demographic parameter	Mean	SD_p	SE_e	Data quality	Data representation
Age-specific survival					
Immature survival (0-4 years) [1]	0.346			2	3
Adult survival [2]	0.910			4	3
Regional-specific productivity					
North – Shetland [3-4]	0.465	0.427		6	4
South – Orkney [3-4]	0.620	0.412		6	4
National-average productivity [3]					
	0.487	0.436		6	4
Age of recruitment [5]					
	4			3	2
Incidence of missed breeding [6]					
	0.030			4	4
Breeding dispersal					
Natal	-			-	-
Adult [2]	Low			-	-

[1]O'Donald 1983; [2]Phillips & Furness 1998; [3]Mavor *et al* 2008; [4]Cook & Robinson 2010; [5]O'Donald & Davis 1975; [6]Catry *et al* 1998.

Recommended demographic rates

The UK estimates of survival for Arctic skua are limited to Shetland (Phillips & Furness 1998, see accompanying material for Arctic skua). The resighting rate in the study by Phillips and Furness (1998) was considered to be high, therefore the bias on true survival rate may be low (Table 16). In the UK, regional differences in population trends could be largely attributed to local differences in breeding success (Cook & Robinson 2010). Consequently, it may be sufficient to assume that the Shetland estimate is representative more broadly (Phillips & Furness 1998; Table 16). Immature survival rates have been estimated based on relatively old productivity, age of maturity and population size data (O'Donald 1983). It may be appropriate to substitute these estimates of survival with those identified for great skua (Table 17), although further matching of local population trends is recommended in order to assess suitability.

Regional trends in productivity rates were identified in two discrete geographic areas (Cook & Robinson 2010; Appendix S3 for map). The productivity of Arctic skua is monitored annually at one SMP Key Site: Fair Isle, and long-term productivity estimates are given for six additional UK localities by Mavor *et al* (2008). The range of productivity values given in Table 16 were calculated using the regional groupings highlighted by Cook and Robinson (2010) to categorise the values specified by Mavor *et al* (2008). These estimates indicate large variability to occur within each region.

Published information on the age of recruitment for Arctic skua is relatively old (O'Donald & Davis 1975), and national census data indicate that the trajectory of the UK population has changed since this estimate was published; from increasing to decreasing (JNCC 2014). Therefore caution should be applied when using the reported age to model current population trends (Table 16). Published information on natal breeding dispersal is conflicting and therefore neither study is included in Table 16 (O'Donald & Davis 1975; Phillips & Furness 1998; see accompanying material for Arctic skua). Adult breeding dispersal has not been quantified, but high mate and site-fidelity indicates that it is low (Phillips & Furness 1998). Local incidence of missed breeding is also low (Catry *et al* 1998).

Population trend in UK
The Arctic skua is a UK BAP species and a red-list Bird of Conservation Concern. The breeding range is restricted to north and west Scotland, and national census data indicate that numbers increased rapidly between 1969 and 1988, but declined between the late 1980s and 2013, possibly more than any other seabird species in the UK (JNCC 2014). Regional differences in population trends were identified in three discrete geographic areas; Shetland, Orkney and North Scotland (Cook & Robinson 2010).

Factors influencing survival rates
Local survival rates are reported to be negatively influenced by decreased prey availability (Davis 2005).

Factors influencing productivity rates
Local productivity rates have been linked to predation from great skuas (Phillips *et al* 1998). They are also relatively low for first time breeders, stabilising from the second breeding attempt (Davis 1976).

Knowledge gaps
The age of recruitment was estimated during a period when the population trajectory differed from the present day. Re-estimation of this parameter could potentially be achieved using the long-term monitoring data from Shetland. Juvenile survival rates are also poorly resolved and rates of adult and natal breeding dispersal are largely unknown. To estimate these demographic parameters would require intensive monitoring and multi-colony studies. Assuming a low rate of natal dispersal, an alternative approach would be to solve for juvenile survival rates based on more recent demographic parameters and population trend data than considered by O'Donald (1983).

5.7.2. Great skua (*Stercorarius skua*)

Table 17. Recommended estimates of demographic rates for the great skua.

Demographic parameter	Mean	SD$_p$	SE$_e$	Data quality	Data representation
Age-specific survival					
Immature survival (0-5 years) [1]	0.730			4	4
Adult survival [1-2]	0.882	0.038		6	4
Colony-specific productivity					
Hermaness [3]	0.800	0.060		6	4
Fetlar [3]	0.740	0.100		6	4
Noss [3]	0.500	0.060		6	4
Mousa [3]	0.670	0.100		6	4
Fair Isle [3]	0.650	0.090		6	4
Foula [3]	0.550	0.080		6	4
North Hill, Papa Westray [3]	0.640	0.080		6	4
Stourdale, Hoy [3]	0.330	0.110		4	4
Handa [3]	0.880	0.200		6	4
National-average productivity [3]					
	0.651	0.308		6	4
Age of recruitment [4]					
	7			2	3
Incidence of missed breeding [5]					
	0.089	0.040		6	4
Breeding dispersal					
Natal [6]	0.015			4	4
Adult [4,7-8]	Low			-	-

[1]Ratcliffe *et al* 2002; [2]Votier *et al* 2004; [3]Mavor *et al* 2008; [4]Furness 1987; [5]Catry *et al* 1998; [6]Klomp & Furness 1992a; [7]Catry & Furness 1997; [8]Catry *et al* 1998.

Recommended demographic rates
The UK estimates of survival for great skua are largely limited to Shetland. However, long term mark-recapture studies are also conducted on Handa and St Kilda. Recently published studies from Foula (Ratcliffe *et al* 2002) and Hermaness (Votier *et al* 2004) reported similar estimates of adult survival. Regional variation in the survival rates of great skuas has not been investigated; therefore the estimate given in Table 17 assumes that the Shetland estimates are representative more broadly. Juvenile and immature survival rates are poorly resolved because few recoveries or resightings are made for these age-classes. The rate provided in Table 17 reflects the total survival between fledging and recruitment (Ratcliffe *et al* 2002).

Regional trends in productivity have been examined using a short-term time series (n=1 year, Phillips *et al* 1997) and therefore would benefit from further analysis (e.g. Cook & Robinson 2010). Consequently, it may be more suitable to use colony-specific rates of productivity to parameterise population models on this species (Table 17). The productivity

of great skua is monitored annually at one SMP Key Site: Fair Isle, and long-term productivity is given for eight additional UK localities by Mavor *et al* (2008).

Published information on the modal age of recruitment for great skua is relatively old and refers to a time when the population was increasing at a faster rate compared to the current trends (Furness 1987; JNCC 2014). The estimate is also considerably older than the estimate for Arctic skua (Table 16). Further consideration is therefore required when parameterising this value in population models. Local incidence of missed breeding is low (Catry *et al* 1998). Breeding dispersal of adults is also very low and any movements within a colony are usually short (Furness *et al* 1987; Catry & Furness 1997; Catry *et al* 1998). Natal breeding dispersal is also reported to be low (Klomp & Furness 1992a).

Population trend in UK
The breeding range of the great skua is restricted to Scotland and concentrated in the Northern Isles. National census data indicate that numbers increased rapidly between 1969 and 1988, this rate of increase then slowed between 1989 and 2002 (JNCC 2014). Regional differences in population trend were noted by Phillips *et al* (1997).

Factors influencing survival rates
The drivers of survival for great skua have not been identified.

Factors influencing productivity rates
Local productivity rates are reported to be negatively influenced by a decrease in prey biomass (Hamer *et al* 1991). The incidence of missed breeding is also higher in years with reduced food availability (Hamer *et al* 1991). There is no evidence that productivity depends on age (Furness 1984; Ratcliffe *et al* 1998).

Knowledge gaps
Information on juvenile and immature survival rates is lacking. Given the low rates of natal dispersal reported (Klomp & Furness 1992a), existing ring-recovery and sighting data should be sufficient to estimate these rates. An alternative approach would be to solve for juvenile survival rates based on other demographic parameters and population trend data collected from a regularly monitored site. Regional variation in survival and productivity rates could also be examined using long-term monitoring data. The age of recruitment would also benefit from re-evaluation using data from key monitoring sites.

5.8. Gulls

5.8.1. Black-legged kittiwake (*Rissa tridactyla*)

Table 18. Recommended estimates of demographic rates for the black-legged kittiwake.

Demographic parameter	Mean	SD_p	SE_e	Data quality	Data representation
Age-specific survival					
Juvenile survival (0-1 year) [1]	0.790			1	3
Adult survival (>2 year) [2-4]	0.854	0.051		6	5
Experience-specific productivity					
1st attempt [5-7]	0.898	0.206		6	4
≥2nd attempt [5-7]	1.379	0.185		6	4
Regional-specific productivity					
Shetland [8-10]	0.408	0.477		6	4
East [8-9,11]	0.819	0.332		6	4
West [8-9]	0.643	0.313		6	4
National-average productivity [8,10-11]					
	0.690	0.296		6	5
Age of recruitment [7,12]					
	4			6	4
Incidence of missed breeding					
Increasing population [13]	0.180	0.188		4	2
Decreasing population [13]	0.208	0.207		4	2
Breeding dispersal					
Natal [12]	0.890			3	3
Adult					
Increasing population [13]	0.012	0.018		6	2
Decreasing population [13]	0.062	0.045		6	2

[1]Coulson & White 1959; [2]Frederiksen *et al* 2004a; [3]Oro & Furness 2002; [4]Taylor *et al* 2010; [5]Coulson & White 1958; [6]Porter 1990; [7]Wooller & Coulson 1977; [8]Mavor *et al* 2008; [9]Frederiksen *et al* 2005; [10]Shaw *et al* 2010; [11]Newell *et al* 2010; [12]Porter & Coulson 1987; [13]Danchin & Monnat 1992.

Recommended demographic rates
The UK estimates of survival for black-legged kittiwake are largely limited to Foula, the Isle of May and Skomer. There are also some older estimates of adult survival from North Shields, NE England (Coulson & Wooller 1976; Aebischer & Coulson 1990; Coulson & Strowger 1999). The most recent colony-specific estimates of survival are from Oro and Furness 2002 (Foula, Shetland), Frederiksen *et al* 2004a (Isle of May, SE Scotland) and Taylor *et al* 2010 (Skomer, Wales). Regional differences in population trends could be largely attributed to local differences in breeding success (Cook & Robinson 2010). Therefore, it may be sufficient to employ a national average for survival when parameterising population models. Juvenile and immature survival rates are poorly resolved because few recoveries or resightings are made for these age-classes. The estimate for juvenile survival

in Table 18 is taken from a short-term ring-recovery study from the 1950s (Coulson & White 1959). National census data indicate that the trajectory of the UK population has changed since this study; from increasing to decreasing (JNCC 2014). Therefore caution should be applied when using this rate to model current population trends, and it may be more appropriate to use estimates based on other gull species (Tables 18-24).

Regional trends in productivity rates were identified in three discrete geographic areas by Cook and Robinson (2010) (Appendix S4 for map), and six discrete geographic areas by Frederiksen *et al* (2005). The productivity of kittiwakes is monitored annually at all four SMP Key Sites: Isle of May, Canna, Fair Isle and Skomer, and long-term productivity estimates are given for 41 additional UK localities by Mavor *et al* (2008). The range of productivity values given in Table 18 were calculated using the regional groupings highlighted by Cook and Robinson (2010) to categorise the values specified by Mavor *et al* (2008). The published information on experience-specific productivity for kittiwake is relatively old (Table 18; Coulson & White 1958; Wooller & Coulson 1977; Porter 1990). These values should be used in population models to guide the proportional change that can be expected with age, as opposed to absolute values of productivity.

Published information on the age of recruitment for black-legged kittiwake is relatively old (Wooller & Coulson 1977), and national census data indicate that the trajectory of the UK population has changed since this study; from increasing to decreasing (JNCC 2014). Therefore caution should be applied when using the reported age to model current population trends (Table 18). The majority of birds breed for the first time at age 4, although a small proportion will start earlier (from age 2), or later (up to age 7; Wooller & Coulson 1977). The incidence of missed breeding in the black-legged kittiwakes has been quantified for two UK colonies; North Shields, NE England (Coulson & White 1956; Coulson & Nève de Mévergnies 1992) and Shetland (Richardson 1985). However, these studies include all non-breeding birds observed in the colony, such as sub-adults, and therefore estimation of non-breeding amongst established breeding pairs is likely to be overestimated. Danchin and Monnat (1992) demonstrate that the incidence of missed breeding in France may reflect the colony trajectory. The values reported in Table 18 are given for colonies with increasing and decreasing population trajectories (Danchin & Monnat 1992). Published estimates of breeding dispersal for adult black-legged kittiwakes in the UK are lacking, although it is expected to be low (Coulson & Strowger 1999; Coulson & Wooller 1976). For populations breeding in France adult dispersal is low, but may vary depending on the local population trajectory and extrinsic conditions (Danchin & Monnat 1992). In contrast, natal dispersal is thought to be high, more so in females (Porter & Coulson 1987; Coulson & Nève de Mévergnies 1992). Although this estimate comes from a relatively old study, high levels of natal dispersal will strongly influence the subsequent population trajectory. This process will require consideration when building population models for this species. Dispersal patterns are also examined by McCoy *et al* (2005) using population genetics.

Population trend in UK
In the UK, the largest black-legged kittiwake colonies are found along the North Sea coasts, around Orkney and Shetland, and off north-west Scotland. National census data indicate that UK colonies increased between 1969 and 1988, but have declined rapidly between the late 1980s and 2013 (JNCC 2014). The national trend was attributed in part to reduced productivity rates (Taylor *et al* 2010). Regional differences in population trends were identified in six discrete geographic areas; Orkney and Shetland, East Scotland and North East England, South East England, South West England, Wales and North East Ireland and West Scotland (Cook & Robinson 2010).

Factors influencing survival rates
Local survival is reported to be positively influenced by prey availability, but negatively influenced by predation from great skuas (Oro & Furness 2002) and winter sea surface

temperatures (Frederiksen *et al* 2004a). Local survival was lower when the sand eel fisheries were active (Frederiksen *et al* 2004a), and was significantly influenced by nesting density (Coulson & Wooller 1976), nest position (Aebischer & Coulson 1990) and algal blooms (Coulson & Strowger 1999). Survival rates do not appear to differ between the sexes (Aebischer & Coulson 1990). For older birds, survival rates apparently decrease, but this could be an artefact of territory-loss, or in earlier studies, ring-loss causing heterogeneity in recapture rates (Aebischer & Coulson 1990; Frederiksen *et al* 2004b).

Factors influencing productivity rates

Local productivity rates are reported to be negatively influenced by a decrease in prey biomass (Hamer *et al* 1993; Harris & Wanless 1990; Lewis *et al* 2001; Oro & Furness 2002; Frederiksen *et al* 2005). Productivity may also decrease following an increase in fishing effort (Lewis *et al* 2001; Frederiksen *et al* 2004a), and increased winter sea surface temperatures (Frederiksen *et al* 2004a). Outside of the UK, studies have shown that local productivity can also be reduced by predation from species such as ravens *Corvus corax* (Danchin & Monnat 1992). There is no evidence that productivity depends on local population size (Frederiksen *et al* 2005). In North Shields, NE England, the productivity of first time breeders was relatively low, stabilising from the second (Wooller & Coulson 1977; Porter 1990) or third breeding attempt (Coulson & White 1958).

Knowledge gaps

The age of recruitment was estimated during a period when the population trajectory differed from the present day. Re-estimation could potentially be achieved using the long-term monitoring data from Foula, Isle of May or Skomer. Juvenile and immature survival rates are largely unknown. High levels of natal dispersal will make this parameter difficult to deduce without multi-colony studies, which would also permit the breeding dispersal of adults to be quantified.

5.8.2. Little gull (*Larus minutus*)

Table 19. Recommended estimates of demographic rates for the little gull.

Demographic parameter	Mean	SD_p	SE_e	Data quality	Data representation
Age-specific survival					
Adult survival [1]	0.800			1	1
Productivity					
	-			-	-
Age of recruitment [2]					
	2-3			4	1
Incidence of missed breeding					
	-			-	-
Breeding dispersal					
Natal	-			-	-
Adult	-			-	-

[1]Garthe & Hüppop 2004; [2]Berg 1937, cited by Cramp & Simmons 1983.

Recommended demographic rates
In the absence of a focused UK program on little gulls, local survival and productivity rates are largely unknown. Published estimates of adult survival are based on similar species (Garthe & Hüppop 2004; Table 19), and published estimates for productivity are lacking completely. Population models should be constructed based on the demographic parameters reported for the other gull species. However, without detailed knowledge on the population trend of this species it will be difficult to assess the suitability of these estimates.

Published information on the age of recruitment for the little gull is relatively old and not based on UK data (Berg 1937, cited by Cramp & Simmons 1983). It was not possible to verify the corresponding population trend for this estimate; however the age is similar to the other estimates reported for small gull species (Tables 19-21). Information on natal and adult dispersal and the incidence of missed breeding is lacking. It may be appropriate to use estimates of dispersal based on black-headed or common gull for population models (Tables 20-21).

Population trend in UK
The little gull is a passage migrant occurring in the UK in both the autumn and the spring (Stone *et al* 1995). During this time they occur mainly offshore, only coming close to shore during strong gales (Wernham *et al* 2002). Therefore exact population trends are unknown.

Factors influencing survival rates
The drivers of survival for little gull have not been identified.

Factors influencing productivity rates
The drivers of productivity for little gull have not been identified.

Knowledge gaps
The demographic parameters of the little gull are largely unknown. Although a small number of birds have been ringed in the UK, more intensive efforts at the breeding grounds would be needed to resolve the local demography of this species.

5.8.3. Black-headed gull (*Chroicocephalus ridibundus*)

Table 20. Recommended estimates of demographic rates for the black-headed gull.

Demographic parameter	Mean	SD$_p$	SE$_e$	Data quality	Data representation
Age-specific survival					
Adult survival (≥2 year) [1-2]	0.825	0.028		6	2
Age-specific productivity					
≤4 breeding attempts [3]	0.683	0.105		6	1
>4 breeding attempts [3]	1.643	0.302		6	1
Colony-specific productivity					
Eilean Inshaig [4]	0.560	0.564		6	4
Sgeir na Caillich [4]	0.490	0.312		6	4
Eilean Ruisg [4]	1.010	0.503		6	4
Airds Islet [4]	0.820	0.791		6	4
Eilean nan Gabhar [4]	0.230	0.325		4	4
Fetla [4]	0.260	0.316		6	4
Egilsay [4]	0.230	0.294		6	4
Shapinsay [4]	0.500	0.380		4	4
Coquet Island [4]	1.230	0.379		6	4
Havergate [4]	0.250	0.014		4	4
Blakeney Point [4]	0.320	0.200		4	4
Scolt Head [4]	0.990	0.191		4	4
Rye Harbour [4]	0.840	0.589		6	4
Langstone Harbour [4]	0.650	0.416		6	4
Hayling Oysterbeds [4]	0.500	0.468		4	4
Brownsea Island [4]	0.510	0.268		6	4
Rockcliffe Marsh [4]	0.200	0.201		6	4
National-average productivity [4]					
	0.625	0.365		6	4
Age of recruitment [3,5]					
	2			6	1
Incidence of missed breeding					
	-			-	-
Breeding dispersal					
Natal	-			-	-
Adult [6]	0.167	0.086		6	1

[1]Majoor *et al* 2005; [2]Péron *et al* 2010; [3]Lebreton *et al* 1990; [4]Mavor *et al* 2008; [5]Prevot-Julliard *et al* 2001; [6]Grosbois & Tavecchia 2003.

Recommended demographic rates

Although a large number of black-headed gulls have been ringed in the UK, ringing often takes place in the winter and away from breeding colonies. These birds may originate from several different breeding colonies, and therefore colony-specific estimates of survival rates are lacking. In France and the Netherlands local adult survival is thought to be relatively constant, although the two estimates differ (Majoor *et al* 2005; Péron *et al* 2010; see accompanying material for black-headed gull). In the absence of UK studies the estimate of adult survival given in Table 20 combined the studies from France and the Netherlands. The local population trends could not be identified, and consequently further consideration is recommended in order to assess the suitability of these estimates. Immature and juvenile survival is poorly resolved because few rings are recovered for this age-class (Robinson & Ratcliffe 2010).

Regional consistency in productivity rates has not been investigated for the black-headed gull (e.g. Cook & Robinson 2010). Consequently, it may be more suitable to use colony-specific rates of productivity to parameterise population models on this species. Long-term productivity is given for 17 UK localities by Mavor *et al* (2008) and there is a marked degree of variation in the reported rates (Table 20). Published information on experience-specific productivity is relatively old and not from the UK (Table 20; Lebreton *et al* 1990). Consequently, these values should be used in population models to guide the proportional change that can be expected with age, as opposed to absolute values of productivity.

Published information on the age of recruitment for black-headed gull is relatively old and not based on UK data (Lebreton *et al* 1990). It was not possible to verify the corresponding population trend for this estimate, however the age is similar to other small gulls (Tables 19-21). Information on the incidence of non-breeding is lacking, but it may be possible to substitute this parameter with values based on the black-legged kittiwake (Table 18). Adult breeding dispersal is thought to be high (Grosbois & Tavecchia 2003), and therefore natal dispersal is also likely to be high.

Population trend in UK

The majority of the UK black-headed gull population are resident throughout the year, and in winter the population are inflated by individuals from Northern and Eastern Europe (Wernham *et al* 2002). National census data indicate that the population was relatively stable between 1985 and 2002, increasing between 2000 and 2013 (JNCC 2014). Regional patterns of change emerged between the 1980s and early 2000s, possibly reflecting the redistribution of birds from coastal to inland colonies (Mitchell *et al* 2004).

Factors influencing survival rates

In France and the Netherlands adult survival rates show little year-to-year variation (Majoor *et al* 2005; Péron *et al* 2010).

Factors influencing productivity rates

Outside of the UK, local productivity rates increase with increased rainfall because this decreases brood predation (Thyen & Becker 2006). The nesting habitat can also be significantly influential (Patterson 1965). The productivity of birds in France was lower during the first three breeding attempts (Lebreton *et al* 1990).

Knowledge gaps

Information on juvenile survival rates, natal dispersal and the incidence of non-breeding is lacking. High levels of natal dispersal will make juvenile survival rates difficult to deduce without multi-colony studies.

5.8.4. Common (or mew) gull (*Larus canus*)

Table 21. Recommended estimates of demographic rates for the common gull.

Demographic parameter	Mean	SD_p	SE_e	Data quality	Data representation
Age-specific survival					
Juvenile survival (0-1 year) [1]	0.410			2	1
Immature survival (1-2 years) [1]	0.710			2	1
Adult survival (>3 year) [2]	0.828	0.050		6	1
Colony specific productivity					
Handa [3]	1.060			4	4
Fair Isle [4]	0.486	0.349		6	5
Mill Dam, Shapinsay [3]	0.010			4	4
Whaness [3]	0.550	0.485		4	4
Sandy Loch [3]	0.950			4	4
Nigg [3]	0.850	0.474		6	4
Bonar Bridge [3]	0.590			4	4
Blakeney Point [3]	0.000	0.000		4	4
Scolt Head [3]	0.200	0.346		4	4
National-average productivity [3-4]					
	0.543	0.391		6	5
Age of recruitment [1]					
	3			4	1
Incidence of missed breeding					
	-			-	-
Breeding dispersal					
Natal					
Male [2]	0.500			4	1
Female [2]	0.900			4	1
Adult [2]	<0.030			4	1

[1]Rattiste & Lilleleht 1987; [2]Rattiste 2004; [3]Mavor *et al* 2008; [4]Shaw *et al* 2010.

Recommended demographic rates

Although a large number of common gulls have been ringed in the UK, ringing often takes place in the winter and away from breeding colonies. These birds may originate from several different breeding colonies, and therefore colony-specific estimates of survival rates are lacking. Published estimates are largely based on mark-recapture studies from Estonia (Rattiste & Lilleleht 1987, 1995; Rattiste 2004). There is also a relatively old ring-recovery study from Denmark (Halling Sørensen 1977). This estimate is considerably lower than those estimated using mark-capture analysis and is therefore likely to be unreliable. Although the values of survival given in Table 21 reflect the most recent estimates, the estimate of juvenile survival is still relatively old (see accompanying material for common gull). The local population trends for these studies could not be identified, consequently

further consideration is recommended in order to assess the suitability of these estimates for modelling UK common gulls.

Regional trends in productivity have not been investigated for this species (e.g. Cook & Robinson 2010). Consequently, it may be more suitable to use colony-specific rates of productivity to parameterise population models on this species. The productivity of the common gull is monitored annually at one SMP Key Sites: Fair Isle, and long-term productivity is given is given for 16 additional UK localities by Mavor *et al* (2008). There is a marked degree of variation in the reported rates (Table 21).

Published information on the age of recruitment for common gull is relatively old and not based on UK data (Rattiste & Lilleleht 1987). It was not possible to verify the corresponding population trend for this estimate, however the age is similar to other small gulls (Tables 19-21). Information on the incidence of non-breeding is lacking but it may be possible to substitute this parameter with values based on the black-legged kittiwake (Table 18). Outside of the UK, adult breeding dispersal is thought to be low (Rattiste 2004), although pairs with less breeding experience are more likely to divorce and disperse after 1 year (*c.* 17–21%), compared to birds with longer breeding experience (*c.* 8–12%). Natal dispersal is high, more so for females (Rattiste 2004). The estimate of natal dispersal comes from a relatively old study, however high levels will strongly influence the subsequent population trajectory. This process requires consideration when building population models for this species.

Population trend in UK
In the UK, breeding populations of common gulls are concentrated in Scotland and Northern Ireland. They breed on coasts and inland sites, dispersing during the winter. Exact population trends are difficult to verify because different methods were used to conduct censuses. Numbers are thought to have increased between 1969 and 2002 (JNCC 2014).

Factors influencing survival rates
Survival of first time breeders is lower during cold winters compared to normal and warm winters (Rattiste & Lilleleht 1995). For older birds (>5 breeding years), survival of males appeared to be slightly higher than for females, but this could reflect lower site fidelity in females (Rattiste & Lilleleht 1995).

Factors influencing productivity rates
Rates of productivity increase with experience (Rattiste 2004), and local productivity rates decrease due to predation from aerial predators (Kilpi 1995).

Knowledge gaps
The survival rates of UK common gulls are poorly resolved, and information on the incidence of non-breeding is lacking. In the absence of a colony-specific ringing program in the UK it will be difficult to improve these estimates using local data. High levels of natal dispersal will make juvenile survival rates difficult to deduce without multi-colony studies.

5.8.5. Lesser black-backed gull (*Larus fuscus*)

Table 22. Recommended estimates of demographic rates for the lesser-black backed gull.

Demographic parameter	Mean	SD$_p$	SE$_e$	Data quality	Data representation
Age-specific survival					
Juvenile survival (0-1 year) [1]	0.820			2	2
Adult survival (≥2 year) [2-3]	0.885	0.022		6	4
Colony-specific productivity					
North Hill [4]	0.800	0.566		4	3
Isle of May [4]	0.880	0.289		6	3
Skomer [4]	0.270	0.165		6	3
Skokholm [4]	0.170	0.066		6	3
Bardsey [4]	0.720	0.221		6	3
National-average productivity [4]					
	0.530	0.325		6	3
Age of recruitment [1]					
	5			4	2
Incidence of missed breeding [5-6]					
	0.337	0.065		4	2
Breeding dispersal					
Natal [7]	0.470			2	2
Adult	-			-	-

[1]Harris 1970; [2]Wanless *et al* 1996; [3]Taylor *et al* 2010; [4]Mavor *et al* 2008; [5]O'Connell *et al* 1997; [6]Calladine & Harris 1997; [7]Coulson 1991.

Recommended demographic rates

The UK estimates of survival for lesser black-backed gull are largely limited to the Isle of May and Skomer. Colony specific estimates of survival appear to differ (see accompanying material for lesser black-backed gull), however regional differences have not been reliably tested. Therefore the estimate of adult survival reported in Table 22 combined the most recent colony-specific studies (Wanless *et al* 1996; Taylor *et al* 2010). Further analysis of regional trends may support the use of colony specific survival rates when parameterising population models for this species. Juvenile and immature survival rates are more difficult to resolve due to lower recovery rates of these age classes. Furthermore, published estimates are relatively old and may not reflect current population trends. It may be more appropriate to use survival estimates based on herring gulls for this age class (Table 23). Further matching of local population trends is recommended in order to assess the suitability of these estimates.

Regional trends in productivity rates have not been investigated for this species (e.g. Cook & Robinson 2010). Consequently, it may be more suitable to use colony-specific rates of productivity to parameterise population models on this species (Table 22). The productivity of the lesser black-backed gull is monitored annually at one SMP Key Site: Skomer, and long-term productivity estimates are given for four additional UK localities by Mavor *et al* (2008).

Published information on the age of recruitment for lesser black-backed gull is relatively old (Harris 1970), and national census data indicate that the trajectory of the UK population has changed since this study; from increasing to decreasing (JNCC 2014). Therefore caution should be applied when using this age to model current population trends (Table 22). The majority of birds breed for the first time at age 5, although a small proportion also breed for the first time at age 3 and 4, and a few individuals may delay breeding until age 6 (Harris 1970). Local incidence of missed breeding is relatively high (Calladine & Harris 1997; O'Connell *et al* 1997). Birds are thought to change breeding locations following failed breeding attempts (Perrins & Smith 2000) and disturbance (O'Connell 1995), indicating that adult breeding dispersal may be high (Ross-Smith *et al* 2014). Natal dispersal is also thought to be high (Coulson 1991).

Population trend in UK
The lesser black-backed gull breeds throughout the UK, and national census data indicate that numbers increased between the late 1960s and early 2000s, but declined during the last decade (JNCC 2014). This trend was attributed in part to a decline in fishery discards (Furness *et al* 1992), and may also reflect the redistribution of birds from coastal to inland colonies (Ross-Smith *et al* 2014).

Factors influencing survival rates
Survival rates do not appear to differ between the sexes (Wanless *et al* 1996), however Bradbury and Griffiths (1999) report a skewed sex-ratio at fledging that could result in more females recruiting to the breeding population.

Factors influencing productivity rates
Local productivity rates have been linked to nesting habitat (Calladine 1997; Kim & Monaghan 2005b), parental condition (Nager *et al* 2000) and fishery discards (Oro 1996).

Knowledge gaps
Information on juvenile survival rates is lacking. High levels of natal dispersal will make this parameter difficult to deduce without multi-colony studies. As with herring gull, a good number of rings are recovered for lesser black-backed gulls. Although this provides a means to estimate annual survival rates, this analysis has yet to be done. There are also a number of colour-marking studies which would provide regional estimates of survival, although these data would need to be collated first, as recommended by Ross-Smith *et al* (2014). The data representation scores on the incidence of missed breeding could also potentially be improved using these data.

5.8.6. Herring gull (*Larus argentatus*)

Table 23. Recommended estimates of demographic rates for the herring gull.

Demographic parameter	Mean	SD$_p$	SE$_e$	Data quality	Data representation
Age-specific survival					
Juvenile survival (0-1 year) [1-2]	0.798	0.092		6	3
Adult survival (≥2 year) [3-4]	0.834	0.034		6	4
Age-specific productivity					
Age 4 [1]	0.000			1	3
Age 5 [1]	0.510			1	3
Age 6 [1]	0.710			1	3
>Age 6 [1]	0.990			1	3
Colony-specific productivity					
Canna [5]	0.740	0.640		6	3
Noss [5]	0.840	0.396		6	3
Isle of May [5]	0.980	0.330		6	3
Skomer [5]	0.770	0.298		6	3
Skokholm [5]	0.700	0.398		6	3
Bardsey [5]	1.220	0.316		6	3
Ynysoedd Gwylan [5]	1.150	0.185		6	3
Walney Island [6]	1.993			4	4
Farne Islands [7]	1.833			4	4
National-average productivity [5-7]					
	0.920	0.477		6	4
Age of recruitment [8]					
	5			4	3
Incidence of missed breeding [9]					
	0.350	0.028		4	3
Dispersal					
Natal [1,10]	0.629	0.156		5	3
Adult	-	-	-	-	-

[1]Chabrzyk & Coulson 1976; [2]Harris 1970; [3]Wanless *et al* 1996; [4]Taylor *et al* 2010; [5]Mavor *et al* 2008; [6]Kim & Monaghan 2005a; [7]Swann 2010; [8]Harris 1970; [9]Calladine & Harris 1997; [10]Coulson 1991.

Recommended demographic rates
The UK estimates of survival for herring gull are largely limited to the Isle of May and Skomer. Older estimates of adult survival include mark-recapture and ring-recovery studies from Lizard Point, Skokholm and Grassholm (Harris 1970; Chabrzyk & Coulson 1976; Coulson & Butterfield 1986). Regional differences in population trends could not be wholly attributed to local differences in breeding success (Cook & Robinson 2010). Regional variation in survival rates is indicated from the colony-specific estimates (see accompanying material for herring gull); however this difference has not been reliably tested. Therefore the

estimate of adult survival reported in Table 23 combined estimates from the most recent colony-specific studies (Wanless *et al* 1996; Taylor *et al* 2010). Further analysis of regional trends may support the use of colony specific survival rates when parameterising population models for this species. Estimates of juvenile and immature survival rates are based on relatively old studies (Table 23; see accompanying material for herring gull). It may be more appropriate to use values based on other large gull species to parameterise the survival rates of these age classes.

Cook and Robinson (2010) could not identify consistent trends in the productivity of herring gulls within the SMP and OSPAR regions. Consequently, it may be more suitable to use colony-specific rates of productivity to parameterise population models on this species (Table 23). The productivity of the herring gull is monitored annually at two SMP Key Sites: Canna and Skomer, and long-term productivity estimates are given for five additional UK localities by Mavor *et al* (2008).

Published information on the modal age of recruitment for the herring gull is available from two studies that were conducted 40 years apart (Harris 1970; Ross-Smith *et al* 2014). The rate of population decline continued during this time (JNCC 2014), and both studies reported a similar age of recruitment (see accompanying material for herring gull). The majority of birds are thought to breed for the first time at age 5, although a small proportion will breed at age 4, and a few individuals may delay until age 6 or 7 (Harris 1970; Ross-Smith *et al* 2014). Local incidence of missed breeding has been estimated using one year of data that is unlikely to be representative more broadly (Calladine & Harris 1997). Information on adult breeding dispersal is lacking, however short-term studies suggest high levels of natal dispersal that may differ between colonies (Chabrzyk & Coulson 1976; Duncan & Monaghan 1977; Coulson 1991). Although this estimate comes from a relatively old study, high levels of natal dispersal will strongly influence the subsequent population trajectory. This process requires consideration when building population models for this species.

Population trend in UK
The herring gull is a UK BAP species and a red-list Bird of Conservation Concern. They are widely distributed around the coasts of the British Isles, and national census data indicate that the UK population continued to decline between 1969 and 2013 (JNCC 2014). During this period the proportion of individuals breeding in the urban environment increased dramatically (Raven & Coulson 1997). More recently, specific colonies have stabilised (e.g. Canna, Swann 2010), and regional patterns of change were identified in four discrete geographic areas; Northern Ireland and Western Scotland, Wales and Western England, Eastern England and Eastern Scotland and North Eastern England (Cook & Robinson 2010).

Factors influencing survival rates
Survival rates do not appear to differ between the sexes (Wanless *et al* 1996).

Factors influencing productivity rates
Local productivity rates have been linked to nesting habitat and parent quality (Kim & Monaghan 2005a), and decrease at low and high nesting densities (Parsons 1976). Productivity increases with age, stabilising from age 6 onwards (Chabrzyk & Coulson 1976).

Knowledge gaps
Regional trends in survival rates could be investigated using the long-term mark-recapture studies from the Isle of May and Skomer. There are also a good amount of ring-recovery data (from birds ringed during the breeding season) that could be used to estimate national, or broad regional, survival rates. A small number of colour-marking studies are also available that could provide an alternative dataset for estimating annual survival rates. Information on adult breeding dispersal is lacking, and the incidence of missed breeding would also benefit

from being re-estimated. Estimation of the incidence of missed breeding could potentially be achieved using the long-term monitoring data from the Isle of May or Skomer.

5.8.7. Great black-backed gull (*Larus marinus*)

Table 24. Recommended estimates of demographic rates for the great black-backed gull.

Demographic parameter	Mean	SD_p	SE_e	Data quality	Data representation
Age-specific survival					
Adult survival [1]	0.930			2	1
Colony-specific productivity					
Canna [2-3]	0.808	0.622		6	5
Noss [2]	0.650	0.268		6	4
North Hill [2]	0.810	0.420		5	4
Brownsea [2]	0.440	0.502		5	4
Skomer [2]	1.290	0.190		6	4
Skokholm [2]	1.150	0.288		6	4
Bardsey [2]	1.840	0.840		6	4
Ynysoedd Gwylan [2]	1.520	0.265		6	4
Rockcliffe Marsh [2]	0.670	0.134		6	4
Big Copeland Island [2]	2.000	-		5	4
National-average productivity [2-3]					
	1.139	0.533		6	5
Age of recruitment [4]					
	5			4	2
Incidence of missed breeding					
	-			-	-
Dispersal					
Natal	-			-	-
Adult	-			-	-

[1]Glutz von Blotzheim & Bauer 1982, cited by Garthe & Hüppop 2004; [2]Mavor *et al* 2008; [3]Swann 2010; [4]Cramp 1985.

Recommended demographic rates
In the absence of a focused UK ringing program on great black-backed gulls, local survival rates are largely unknown. Published estimates of adult survival include a relatively old study from Germany (Glutz von Blotzheim & Bauer 1982, cited in Garthe & Hüppop 2004; see accompanying material for great black-backed gull). Juvenile and immature survival rates are also unknown. Population models should be constructed based on the demographic estimates reported for the other large gull species. However, further matching of local population trends is recommended in order to assess the suitability of these estimates.

Regional trends in productivity rates have not been investigated for this species (e.g. Cook & Robinson 2010). Consequently, it may be more suitable to use colony-specific rates of productivity to parameterise population models on this species (Table 24). The productivity of great black-backed gulls is monitored annually at two SMP Key Sites: Canna and Skomer, and long-term productivity estimates are given for seven additional UK localities by Mavor *et al* (2008).

Published information on the age of recruitment for great black-backed gulls is relatively old and may not be based on UK data (Cramp 1985). The age of first breeding is thought to be between 4 and 5 years (Cramp 1985). National census data indicate that the rate of decrease for the UK population has changed since this estimate was published (JNCC 2014). Therefore caution should be applied when using this age to model current population trends (Table 24). Information on natal and adult dispersal and the incidence of missed breeding is lacking and estimates based on herring gull (Table 23) could be used to represent these. Matching of local population trends is recommended to assess the suitability of these estimates.

Population trend in UK
Great black-backed gulls breed mainly in the Outer and Inner Hebrides and the Northern Isles of Scotland. National census data indicate that colonies were declining slowly between 1960 and 2002, and more quickly between 2000 and 2013 (JNCC 2014). This earlier trend was partially attributed to a decline in fishery discards (Furness *et al* 1992).

Factors influencing survival rates
The drivers of survival for great black-backed gulls have not been identified.

Factors influencing productivity rates
Local productivity rates decrease due to predation from mink, albeit to a lesser extent than observed in the smaller gull species (Craik 2013). Outside of the UK, productivity rates have been linked to nesting density (Butler & Trivelpiece 1981; Ellis & Good 2006), laying dates (Regehr & Rodway 1999), nesting habitat (Ellis & Grid 2006) and contaminants (Helberg *et al* 2005).

Knowledge gaps
Information on juvenile and immature survival rates, natal and adult dispersal, and the incidence of missed breeding are all lacking. There are some ring-recovery data for birds ringed during the breeding season (primarily as chicks) that have the potential to provide estimates of annual survival rates, but these data have not yet been analysed in this way. The ability to resolve juvenile survival from these estimates will depend on levels of natal dispersal.

5.9. Terns

5.9.1. Sandwich tern (*Sterna sandvicensis*)

Table 25. Recommended estimates of demographic rates for the Sandwich tern.

Demographic parameter	Mean	SD$_p$	SE$_e$	Data quality	Data representation
Age-specific survival					
Juvenile survival (0-1 year) [1]	0.358		0.219	4	4
Immature survival (2-3-4 years)[1]	0.741		0.206	4	4
Adult survival [1]	0.898		0.029	4	4
Age-specific productivity					
Age 3 years [2]	*0.167			2	1
Age 4 years [2]	*0.235			2	1
Age 5-11 years [2]	*0.649			2	1
Colony-specific productivity					
Sands of Forvie [3]	0.560	0.440		6	3
Coquet [3]	0.600	0.240		6	3
Scolt Head [3]	0.690	0.400		6	3
Blakeney [3]	0.690	0.320		6	3
Rye Harbour [3]	0.570	0.620		6	3
Langstone Harbour [3]	0.470	0.330		6	3
Brownsea [3]	0.670	0.392		6	3
Anglesey [3]	0.870	0.271		6	3
Hodbarrow [3]	0.480	0.480		6	3
Lough Swilly [3]	1.030	0.313		6	3
Mulroy Bay [3]	0.920	0.397		6	3
Lady's Island Lake [3]	0.800	0.265		6	3
National-average productivity [3]					
	0.702	0.372		6	3
Age of recruitment [2]					
	3			2	1
Incidence of missed breeding					
	-			-	-
Breeding dispersal					
Natal	-			-	-
Adult	-			-	-

[1]Robinson 2010; [2]Veen 1977; [3]Mavor *et al* 2008. * Maximum values (see text).

Recommended demographic rates
The size of Sandwich tern colonies can fluctuate significantly between years as birds redistribute between adjacent colonies (Lloyd *et al* 2001). High adult dispersal complicates

the ability to reliably resolve population trends and survival rates without multi-colony studies. In the absence of a focused UK ringing program on Sandwich terns, colony-specific survival rates are not available. Published estimates are based on similar species (Garthe & Hüppop 2004), and two ring-recovery studies from the UK (Green *et al* 1990; Robinson 2010) (see accompanying material for Sandwich tern). National census data indicate that the trajectory of the UK population has changed since the Green *et al* (1990); from increasing to decreasing (JNCC 2014). Therefore the estimate for adult survival in Table 25 is based on Robinson (2010). Regional variation in survival rates has not been investigated; however regional differences in population trends could not be wholly attributed to local differences in breeding success (Cook & Robinson 2010). At present there are not sufficient data to model colony-specific survival rates for Sandwich tern. It is important to consider these regional differences in population trend as caveats of any population models developed.

Cook and Robinson (2010) could not identify consistent regional trends in the productivity of Sandwich terns within the SMP and OSPAR regions. Consequently, it may be more suitable to use colony-specific rates of productivity to parameterise population models on this species. Long-term productivity is given for 12 localities in the UK by Mavor *et al* (2008). Published information on experience-specific productivity for Sandwich tern is relatively old (Table 25; Veen 1977). These values should be used in population models to guide the proportional change that can be expected with age, as opposed to absolute values of productivity. These estimates are maximum values only because they do not account for multiple chicks being fledged per pair.

Published information on the modal age that Sandwich terns breed for the first time is lacking. In the Netherlands, 3 year old but not 2 year old birds were reported in the breeding population (Veen 1977). This study is relatively old and it was not possible to verify the corresponding population trend, however the reported age is similar to other tern species (Tables 25-28). Although adult dispersal is known to be high (Lloyd *et al* 2001), rates have not been quantified. Information on the incidence of missed breeding and natal breeding dispersal are also currently lacking. It may be possible to substitute these parameters with values from the other tern species. Further matching of local population trends is recommended in order to assess the suitability of these estimates.

Population trend in UK
Sandwich tern colonies occur in a patchy distribution throughout the British coastline. National census data indicate that colonies increased between 1969 and 1988, decreased between the late 1980s and early 2000s and stabilised between 2000 and 2013 (JNCC 2014). Regional patterns of change were identified in five discrete geographic areas; the East of Scotland, the East of England, the South East of England, Wales, South and South West of England and the North Irish Sea (Cook & Robinson 2010).

Factors influencing survival rates
The drivers of survival for Sandwich tern have not been identified.

Factors influencing productivity rates
In the Netherlands, local productivity rates decrease due to predation from gulls (Veen 1977). Furthermore, mean clutch size and hatching success increase with age (Veen 1977).

Knowledge gaps
The survival rates of Sandwich terns are not reliably resolved, and information on natal and adult dispersal and the incidence of missing breeding is also lacking. In the absence of a focused UK ringing program it will be difficult to improve these estimates using local data.

5.9.2. Common tern (*Sterna hirundo*)

Table 26. Recommended estimates of demographic rates for the common tern.

Demographic parameter	Mean	SD$_p$	SE$_e$	Data quality	Data representation
Age-specific survival					
Immature survival (0-2 years) [1]	0.441		0.004	4	1
Immature survival (3-4 years) [2]	0.850			4	1
Adult survival (≥6 year) [2-3]	0.883	0.014		6	1
Colony-specific productivity					
E an Ruisg, L Feochan [4]	1.820	0.594		6	3
Sgeir na Caillich, L Melfort [4]	0.670	0.688		6	3
G. Eileanan, Sd Mull [4]	0.530	0.529		6	3
Avoch Fish Farm [4]	0.770	0.563		6	3
St Fergus [4]	0.150	0.173		6	3
Forth [4]	0.910	0.381		6	3
Coquet [4]	1.030	0.626		6	3
Rye Meads [4]	0.530	0.411		6	3
Hoveton Great Broad [4]	0.260	0.291		6	3
Snettisham [4]	0.280	0.374		6	3
Holkham [4]	0.400	0.503		6	3
Blakeney [4]	0.440	0.469		6	3
Breydon Water [4]	0.990	0.252		6	3
Pitts Deep – Hurst [4]	0.370	0.311		6	3
Langstone Harbour [4]	0.540	0.552		6	3
Rye Harbour [4]	1.050	0.716		6	3
Brownsea Is. [4]	0.590	0.289		6	3
Lodmoor [4]	1.460	0.509		6	3
Shotton [4]	1.300	0.495		6	3
Cemlyn [4]	0.590	0.720		6	3
Seaforth [4]	0.610	0.313		6	3
Rockcliffe [4]	0.110	0.180		6	3
Belfast Lough [4]	1.350	0.313		6	3
Rockabill [4]	1.590	0.465		6	3
National-average productivity [4]					
	0.764	0.470		6	3
Age of recruitment [5-6]					
	3-4			6	1
Incidence of missed breeding [7]					
	Low			-	-

Demographic parameter	Mean	SD_p	SE_e	Data quality	Data representation
Breeding dispersal					
Natal [3]	0.070			2	1
Adult [2-3]	0.103	0.077		6	1

[1]Braasch *et al* 2008; [2]Breton *et al* 2014; [3]Nisbet & Cam 2002; [4]Mavor *et al* 2008; [5]Nisbet 1978; [6]Ludwigs & Becker 2002a; [7]Dittmann *et al* 2002.

Recommended demographic rates
In the absence of a focused UK ringing program on common terns, local survival rates are largely unknown. There are relatively old published estimates from North America; including three mark–recapture studies based on constant recapture rates (Austin & Austin 1956; Nisbet 1978; DiCostanzo 1980). More recent studies from North America model survival rates using variable recapture rates (Nisbet & Cam 2002; Breton *et al* 2014). Regional variation in the survival rates of common terns has not been investigated. Therefore the estimate of adult survival in Table 26 combined estimates from the two most recent colony-specific studies (see accompanying material for common tern). The local population trend could not be identified for these studies, therefore further matching of local population trends is recommended in order to assess their suitability for modelling the UK population. Estimates of juvenile survival are limited to relatively short-term studies (DiCostanzo 1980; Braasch *et al* 2008). The more recent of these was used to represent juvenile survival in Table 26.

Regional trends in productivity have not been investigated for this species (e.g. Cook & Robinson 2010). Consequently, it may be more suitable to use colony-specific rates of productivity to parameterise population models on this species (Table 26). Long-term productivity is given for 24 localities in the UK by Mavor *et al* (2008).

Published information on the age of recruitment is regionally specific. In Germany, common terns are thought to breed for the first time at age 3 (Ludwigs & Becker 2002a), and in North America the age of first breeding is thought to occur at age 4 (Nisbet 1978). Further matching of local population trends is recommended in order to assess the suitability of these estimates for modelling the UK population. The incidence of missed breeding is thought to be low (Dittmann *et al* 2002), although population rates have not been quantified. The dispersal of adult common terns is predominantly low, but may vary between colonies (González-Solís *et al* 1999; Nisbet & Cam 2002) and increase between colonies that are closely distributed (Breton *et al* 2014). Natal dispersal is also thought to be low (Nisbet & Cam 2002). The rates of dispersal listed in Table 26 reflect the number of studies that quantify this parameter. Dispersal is reported to be higher for adults compared to the natal age class, but this is unlikely to occur in reality. For the local difference between these age classes see Nisbet and Cam (2002).

Population trend in UK
Common terns breed throughout much of the British coastline and larger inland waterbodies. National census data indicate that colonies were relatively stable between 1969 and 2002, but declined between 2000 and 2013 (JNCC 2014).

Factors influencing survival rates
Outside of the UK, survival rates were relatively constant through time (Breton *et al* 2014), and do not appear to differ between the sexes (Braasch *et al* 2008; Breton *et al* 2014). Breton *et al* (2014) report that survival rates follow a quadratic relationship with age; increasing between fledging and recruitment, stabilising for a number of years, and then declining when individuals are >12 years old. There was no evidence that local survival from

fledging to first breeding depends on hatching order, hatching date, number of fledglings per brood or parental age (Nisbet 1996; Dittmann *et al* 2001). First year survival increased with fledging mass (Ludwigs & Becker 2002b).

Factors influencing productivity rates
Local productivity rates decrease due to predation (Nisbet & Welton 1984; Becker 1995; Mavor *et al* 2008) and increased nesting density (Becker 1995). Productivity also depends on parental age or quality (Bollinger 1994; Wendeln & Becker 1999; Nisbet *et al* 2002; Arnold *et al* 2006).

Knowledge gaps
Age-specific survival rates and natal breeding dispersal are largely unknown for the UK population. The incidence of missed breeding is also poorly resolved. In the absence of a focused UK ringing program on common terns it will be difficult to improve these estimates using local data.

5.9.3. Arctic tern (*Sterna paradisaea*)

Table 27. Recommended estimates of demographic rates for the Arctic tern.

Demographic parameter	Mean	SD_p	SE_e	Data quality	Data representation
Age-specific survival					
Adult survival ($\geq$2 year) [1-2]	0.837	0.035		6	2
Colony-specific productivity					
Ardullie [3]	0.780	0.156		4	3
Coquet [3]	0.770	0.320		6	3
Eigg [3]	0.120	0.170		6	3
Fair Isle [4]	0.125	0.210		6	4
Farne Islands [3]	0.570	0.348		6	3
Fetlar [3]	0.130	0.194		6	3
Foula [5]	0.238	0.288		6	4
Foulney [3]	0.350	0.224		6	3
Isle of May [3]	0.310	0.277		6	3
Kinloss [3]	0.160	0.232		6	3
Long Nanny [3]	0.660	0.480		6	3
Papa Westray [3]	0.160	0.312		6	3
Rockabill [3]	0.870	0.379		6	3
Sands of Forview [3]	0.260	0.310		6	3
Skerries [3]	1.080	0.400		6	3
St Fergus [3]	0.090	0.108		6	3
Tiree [3]	0.030	0.073		6	3
National-average productivity [3-5]					
	0.380	0.325		6	4
Age of recruitment [1,2]					
	4			6	3
Incidence of missed breeding					
	-			-	-
Breeding dispersal					
Natal [6]	0.610			4	1
Adult [6-7]	0.089	0.115		6	1

[1]Cullen 1957; [2]Coulson & Horobin 1976; [3]Mavor *et al* 2008; [4]Shaw *et al* 2010; [5]Furness 2007; [6]Devlin *et al* 2008; [7]Møller *et al* 2006.

Recommended demographic rates
The UK estimates of adult survival for Arctic tern are largely limited to the Farne Islands (Cullen 1957; Coulson & Horobin 1976). More recent estimates of survival are from Canada (Devlin *et al* 2008). Regional differences in survival have not been investigated; however the rates of survival reported for the UK and Canada are relatively similar (see accompanying material for Arctic tern). The estimate given in Table 27 combined the UK estimates. National census data indicate that the trajectory of the UK population has changed since

these publications, from increasing to decreasing (Shaw *et al* 2010; JNCC 2014). Therefore caution should be applied when using these rates to model current population trends.

Regional trends in productivity rates have not been investigated for this species (e.g. Cook & Robinson 2010). Consequently, it may be more suitable to use colony-specific rates of productivity to parameterise population models on this species (Table 27). The productivity of Arctic tern is monitored annually at one SMP Key Site: Fair Isle, and long-term productivity is given for 15 additional UK localities by Mavor *et al* (2008).

Information on the age of recruitment for Arctic tern is relatively old, and the national population trend is thought to have changed since it was published (Cullen 1957; Coulson & Horobin 1976). The majority of Arctic terns breed for the first time at age 4, although a small proportion breed for the first time at age 5, and a few individuals may also attempt breeding at 2 or 3 years old (Cullen 1957; Coulson & Horobin 1976). The reported modal age is older than for the other terns (Tables 25-28), and therefore some caution should be applied when using this estimate to model current population trends. Information on the incidence of missed breeding is limited, although it is thought to occur primarily in response to food shortage (Monaghan *et al* 1992). Outside of the UK, breeding dispersal of adult Arctic terns is low (Møller *et al* 2006; Devlin *et al* 2008), although it is higher between colonies that are closely distributed (Brindley *et al* 1999; Møller *et al* 2006; Devlin *et al* 2008). Adult and natal dispersal are also thought to reflect local conditions at a colony, e.g. low levels of food availability can increase dispersal (Møller *et al* 2006). Further matching of local population trends is recommended in order to assess the suitability of these estimates for modelling UK birds. In Denmark, natal dispersal is thought to be high (Møller *et al* 2006). This process will strongly influence the subsequent population trajectory, and therefore requires consideration when building population models for this species.

Population trend in UK
Breeding colonies of Arctic terns are concentrated in the Northern Isles. Exact population trends are difficult to verify because different methods were used to conduct censuses. Numbers are thought to have increased between 1969 and 1988, decreased between 1988 and 2002, and stabilised between 2000 and 2013 (Shaw *et al* 2010; JNCC 2014).

Factors influencing survival rates
The drivers of survival for Arctic tern have not been identified.

Factors influencing productivity rates
Local productivity rates are reported to be positively influenced by increased prey abundance (Monaghan *et al* 1989; Suddaby & Ratcliffe 1997; Robinson *et al* 2001; Furness 2007) and negatively influenced by predation (Nordström *et al* 2004; Mavor *et al* 2008). Nest location can also be significantly influential (Bunin & Boates 1994). Mean clutch size may increase in relation to age, although small sample sizes prevented this from being reliably quantified (Coulson & Horobin 1976). Monaghan *et al* (1989) demonstrated that the productivity of Arctic terns differed between colonies in relation to foraging conditions.

Knowledge gaps
Estimates of juvenile and immature survival are lacking. High levels of natal dispersal will make these parameters difficult to deduce without multi-colony studies. A population rate for the incidence of missed breeding has also not been quantified. More intensive efforts at the breeding ground would be needed to resolve this parameter.

5.9.4. Little tern (*Sternula albifrons*)

Table 28. Recommended estimates of demographic rates for the little tern.

Demographic parameter	Mean	SD$_p$	SE$_e$	Data quality	Data representation
Age-specific survival					
Adult survival [1]	0.800			3	2
Regional-specific productivity					
North [2-3]	0.456	0.482		6	4
South [2-3]	0.464	0.506		6	4
National-average productivity [2]					
	0.518	0.518		6	4
Age of recruitment [4]					
	>2			2	2
Incidence of missed breeding					
	-			-	-
Breeding dispersal					
Natal	-			-	-
Adult	-			-	-

[1]Grosskopf 1964, cited by Robinson & Ratcliffe 2010; [2]Mavor *et al* 2008; [3]Cook & Robinson 2010; [4]Schönert 1961, cited by Cramp 1985.

Recommended demographic rates
In the absence of a focused UK ringing program on little terns, local survival rates are largely unknown (see accompanying material for little tern). Outside of the UK, published estimates include a relatively old ring-recovery study (Grosskopf 1964, cited by Robinson & Ratcliffe 2010). Regional differences in population trends could not be wholly attributed to local differences in breeding success (Cook & Robinson 2010). At present there are not sufficient data to model colony-specific survival rates, and therefore it will be important to consider regional differences in population trend as caveats of population models that are developed.

Regional trends in productivity rates were identified by Cook and Robinson (2010) in two discrete geographic areas (see Appendix S5 for map). Long-term productivity is given for 21 localities in the UK by Mavor *et al* (2008). The range of productivity values given in Table 28 were calculated using the regional groupings highlighted by Cook and Robinson (2010) to categorise the values specified by Mavor *et al* (2008). These estimates indicate large variability to occur within each region.

Published estimates for the age of recruitment of little tern is relatively old and not based on UK data. Little terns are thought to start breeding at a minimum of 2 years, usually older (Schönert 1961, cited by Cramp 1985). This minimum age is lower than the modal ages that were identified for the other tern species (Tables 25-28). It therefore may not be representative of the modal age for little tern. Information on natal and adult dispersal and the incidence of missed breeding is largely lacking. It may be possible to use estimates based on common tern or Arctic tern (Table 26; Table 27) to represent these demographic parameters. Matching of local population trends is recommended in order to assess the suitability of these estimates.

Population trend in UK
Little tern colonies are scattered along much of the British coastline, but the main concentration is in the south and east of England. In the UK, abundance generally declined after the late 1980s but stabilised in the 1990s (Ratcliffe *et al* 2000). The decline was attributed to low rates of productivity (Ratcliffe *et al* 2000). The rate of decline varies regionally in four discrete geographic areas; East Scotland and North East England, East and South England, Wales and West England and West Scotland and East Ireland (Cook & Robinson 2010).

Factors influencing survival rates
The drivers of survival for little tern have not been identified.

Factors influencing productivity rates
Local productivity rates have been linked to human disturbance (Medeiros *et al* 2007; Perrow *et al* 2011) and nest location (Oro *et al* 2004).

Knowledge gaps
Rates of survival and the age of recruitment are poorly resolved. The incidence of missed breeding and rates of breeding dispersal are also largely unknown. In the absence of a focused UK ringing program on little tern it will be difficult to improve these estimates using local data.

5.10. Auks

5.10.1. Common guillemot (*Uria aalge*)

Table 29. Recommended estimates of demographic rates for common guillemot.

Demographic parameter	Mean	SD$_p$	SE$_e$	Data quality	Data representation
Age-specific survival					
Juvenile survival (0-1 year) [1]	0.560		0.013	6	3
Immature survival (1-2 year) [1]	0.792		0.034	6	3
Immature survival (2-3 year) [1]	0.917		0.022	6	3
Adult survival ($\geq$4th year) [2-4]	0.939	0.015		6	6
Experience-specific productivity					
1st year [5]	0.620			6	3
$\geq$2nd year [5]	0.686	0.068		6	3
Regional-specific productivity					
North [6-8]	0.629	0.174		6	5
East [6-7,9]	0.659	0.133		6	5
West [4,6-7]	0.823	0.056		6	5
National average productivity [4,6,8-9]					
	0.672	0.147		6	5
Age of recruitment [10]					
	6			6	4
Incidence of missed breeding [11]					
	0.079			6	3
Dispersal					
Natal [1,12]	0.580	0.212		6	3
Adult [13]	0.007			4	3

[1]Harris *et al* 2007; [2]Lahoz-Monfort *et al* 2011; [3]Reynolds *et al* 2011; [4]Meade *et al* 2013; [5]Crespin *et al* 2006a; [6]Mavor *et al* 2008; [7]Cook & Robinson 2010; [8]Shaw *et al* 2010; [9]Newell *et al* 2010; [10]Halley & Harris 1993; [11]Harris & Wanless 1995; [12]Harris *et al* 1996; [13]Swann & Ramsay 1983.

Recommended demographic rates
The UK estimates of survival for common guillemot are largely limited to the Isle of May, Canna, Colonsay and Skomer. Regional differences in abundance trends were largely attributed to local differences in breeding success (Cook & Robinson 2010) and colonies with increasing and decreasing trends report adult survival rates to be similar (e.g. Isle of May – Reynolds *et al* 2011; Skomer - Meade *et al* 2013) (see accompanying material for common guillemot). Therefore, it may be sufficient to employ a national average for survival when parameterising population models of common guillemot. However, it should be noted that inter-colony comparisons of survival rates demonstrate some evidence of regional differences (Harris *et al* 2000b). A high correlation is thought to occur between breeding colonies that share wintering areas (Reynolds *et al* 2011). To apply colony-specific survival rates to population models, preference should be given to survival rates from colonies that overlap in winter distribution. The estimate of adult survival reported in Table 29 combined

estimates from the most recent colony-specific studies. Stronger metal rings were introduced in Britain and Ireland in 1983 to reduce ring-loss and wear to the inscription associated with standing on rocky cliff-ledges. Therefore, unless survival estimates have been corrected for ring loss, only more recent estimates can be reliably used. Immature guillemots tend to revisit their natal colony at least once before recruiting to a breeding population. Therefore estimates of immature survival rate derived from mark-recapture data should be reliable when accompanied by extensive recapture effort (e.g. Harris *et al* 2007). Other estimates of juvenile survival from the Isle of May (Crespin *et al* 2006a) and Canna (Reynolds *et al* 2011) are detailed in the accompanying material for common guillemot.

Regional trends in productivity rates were identified in three discrete geographic areas (Cook & Robinson 2010; Appendix S6 for map). The productivity of common guillemot is monitored annually at three SMP Key Sites: Isle of May, Fair Isle and Skomer, and long-term productivity estimates are given for eight additional UK localities by Mavor *et al* (2008). The range of productivity values given in Table 29 were calculated using the regional groupings highlighted by Cook and Robinson (2010) to categorise the values specified by Mavor *et al* (2008), Shaw *et al* (2010), Newell *et al* (2010) and Meade *et al* (2013). The estimates of experience-specific productivity in Table 29 should be used to guide the proportional change that can be expected with age, as opposed to absolute values of productivity.

Published information on the age of recruitment for common guillemot is relatively old, and differs regionally. On Skomer and the Isle of May the median age of first breeding appeared to be one or two years earlier than on Canna (Birkhead & Hudson 1977; Halley & Harris 1993; Harris *et al* 1994a). This may reflect differences in methodology. Daily monitoring on the Isle of May minimises the bias caused by birds losing eggs soon after laying (Harris *et al* 1994a). Therefore, the value in Table 29 is based on the Isle of May estimate only. The incidence of missed breeding in the common guillemot was explored extensively by Harris and Wanless (1995). The behaviour seemed to vary between individuals, with 6% of individuals accounting for 47% of non-breeding cases (n=146). The occurrence of adult dispersal is low (Swann & Ramsay 1983) but increases between closely distributed colonies (Southern *et al* 1965). Natal dispersal is considerably higher (Swann & Ramsay 1983; Harris *et al* 1996; Harris *et al* 2007). The rates of natal dispersal in Table 29 are from the multi-colony study by Harris *et al* (1996). High levels of natal dispersal will strongly influence the subsequent population trajectory, and requires consideration when building population models for this species.

Population trend in UK
The common guillemot is the most abundant breeding seabird in the UK (Mitchell *et al* 2004). Populations increased rapidly in all regions of the UK between 1969 and 1985. This rate of increase slowed between 1985 and 2002, and then slowed again between 2000 and 2013 (JNCC 2014). In the early 1980s, regional differences emerged in two discrete geographic areas; the East Coast of the UK and the second on the West Coast of the UK (Cook & Robinson 2010; Heubeck & Mellor 2014). On Skomer Island numbers have increased at an almost constant rate of 5% per annum in the last 30 years (Meade *et al* 2013). In contrast, colonies on the Isle of May, Fair Isle and Canna are presently in decline (Harris *et al* 1996; Newell *et al* 2010; Swann 2010).

Factors influencing survival rates
Local survival rates have been linked to oil pollution and also the marine environment; decreasing at high values of winter Northern Atlantic Oscillation (i.e. survival rates are lower following warmer sea temperatures and stronger winds, Votier *et al* 2005, 2008). On the Isle of May (SE Scotland) there is no evidence that survival depends on prey density or local population size (Harris *et al* 2007). For older birds, survival begins to decline at >19 years (Crespin *et al* 2006a).

Factors influencing productivity rates

Local productivity rates are reported to be negatively influenced by decreased prey biomass (Rindorf *et al* 2000; Wanless *et al* 2005). Productivity also increases with greater synchrony of lay dates, although there was no evidence for an effect of the actual lay date (Birkhead 1977a). Productivity of first time breeders was relatively low, stabilising from the fifth attempt and decreasing when birds breed for >13 years (Crespin *et al* 2006a).

Knowledge gaps

The demography of guillemots in the UK is relatively well resolved.

5.10.2. Razorbill (*Alca torda*)

Table 30. Recommended estimates of demographic rates for the razorbill.

Demographic parameter	Mean	SD$_p$	SE$_e$	Data quality	Data representation
Age-specific survival					
Immature survival (0-2 years) [1]	0.630	0.209		6	2
Adult survival (≥3 year) [2-3]	0.895	0.067		6	6
Regional-specific productivity					
South [4-6]	0.642	0.271		6	4
Mid [4-5,7]	0.643	0.057		6	5
North [4-5,8]	0.459	0.236		6	5
National-average productivity [4,6-8]					
	0.570	0.247		6	5
Age of recruitment [9]					
	5			3	3
Incidence of missed breeding [10]					
	0.030			4	3
Dispersal					
Natal [9,11]	0.088	0.116		5	3
Adult [10-12]	0.047	0.046		5	3

[1]Lavers *et al* 2008; [2]Taylor *et al* 2010; [3]Lahoz-Monfort *et al* 2011; [4]Mavor *et al* 2008; [5]Cook & Robinson 2010; [6]Lloyd 1979; [7]Newell *et al* 2010; [8]Shaw *et al* 2010; [9]Lloyd & Perrins 1977; [10]Harris & Wanless 1989; [11]Lavers *et al* 2007; [12]Lloyd 1976.

Recommended demographic rates

The UK estimates of survival for razorbill are largely limited to the Isle of May and Skomer. There is also an older estimate based on shorter-term data from the Shiant Islands, NW Scotland (Chapdelaine 1997, see accompanying material for razorbill). Estimates of adult survival from outside of the UK appear to be higher (Sandvik *et al* 2005; Lavers *et al* 2008). Regional differences in population trends could be largely attributed to local differences in breeding success (Cook & Robinson 2010), therefore it may be sufficient to employ a national average for survival when parameterising population models of this species. Although the estimate given in Table 30 combined the most recent UK studies, information on juvenile and immature survival rates is limited to a relatively old ring-recovery study (Lloyd 1974). National census data indicate that the trajectory of the UK population has changed since this study; therefore the estimate of immature survival in Table 30 is taken from a more recent mark-recapture study from Canada (Lavers *et al* 2008). Although razorbills in Canada were following a similar population trend to the current UK population; the estimate of adult survival by Lavers *et al* (2008) is higher than the estimate reported for the UK by Lahoz-Monfort *et al* (2011) and Taylor *et al* (2010). Therefore caution should be applied when using these estimates to model the current UK population trend.

Regional differences in productivity were identified by Cook and Robinson (2010) in three discrete geographic areas (Appendix S7 for map). The productivity of razorbill is monitored annually at three SMP Key Sites: Isle of May, Skomer and Fair Isle, and long-term productivity estimates are given for four additional UK localities by Mavor *et al* (2008). The

range of productivity values given in Table 30 were calculated using the regional groupings highlighted by Cook and Robinson (2010) to categorise the values specified by Lloyd (1979), Mavor *et al* (2008), Newell *et al* (2010) and Shaw *et al* (2010).

Published information on the age of recruitment for the razorbill is relatively old and may vary regionally in relation to nest site availability (anecdotal evidence reviewed by Lloyd & Perrins 1977). The reported age is similar to the other auk species (Tables 29-32), and consequently may be suitable for modelling current population trends. Local incidence of missed breeding is low (Harris & Wanless 1989), but the behaviour is more prevalent in certain individuals (Harris & Wanless 1989). Adult dispersal is also thought to be very low (Lloyd 1976; Harris & Wanless 1989; Lavers *et al* 2007). At a stable UK colony, natal dispersal was reported to be very low (Lloyd & Perrins 1977), but in Canada rates were higher (Lavers *et al* 2008). To represent the range of adult and natal dispersal, the value given in Table 30 combined estimates from the UK and Canada (see accompanying material for razorbill).

Population trend in UK
The UK population increased between 1969 and 2002 (JNCC 2014), however this trend varies regionally, for example particular colonies declined during the 1990s, before stabilising or increasing during the last decade (Shaw *et al* 2010; Swann 2010). On Canna this change in trajectory followed the successful eradication of rats (Swann 2010). Regional differences in abundance trends were identified in four discrete geographic areas; the East Coast of Scotland, the South Coast of Wales, the North Coast of Wales and the West Coast of Scotland (Cook & Robinson 2010).

Factors influencing survival rates
Survival rates have been linked to the marine environment, and decrease at high values of winter Northern Atlantic Oscillation (i.e. survival rates are lower following warmer sea temperatures and stronger winds, Sandvik *et al* 2005). The survival rates of razorbills do not appear to differ between the sexes (Harris *et al* 2000a).

Factors influencing productivity rates
Local productivity rates decline in response to predation from gulls (Hudson 1982).

Knowledge gaps
Juvenile and immature survival rates are poorly resolved for UK populations. Assuming low levels of natal dispersal (Lloyd & Perrins 1977), it should be possible to estimate these rates using existing ring-recovery and sighting data. An alternative approach would be to solve for juvenile survival rates based on other demographic parameters and population trend data collected from a regularly monitored site (e.g. Skomer or Isle of May).

5.10.3. Black guillemot (*Cepphus grylle*)

Table 31. Recommended estimates of demographic rates for black guillemot.

Demographic parameter	Mean	SD_p	SE_e	Data quality	Data representation
Age-specific survival					
Juvenile survival (0-1 year) [1]	0.731	0.239		6	2
Adult survival [1]	0.870	0.034		6	2
Colony-specific productivity					
North Ronaldsay [2]	1.420	0.316		6	4
Auskerry [2]	1.310	0.166		6	4
Swona [2]	1.500	0.201		6	4
Old Lighthouse Island [2]	1.080	0.280		6	4
Mew Island [2]	2.000			4	4
Rockabill [2]	1.260	0.226		6	4
National-average productivity [2]					
	1.298	0.315		6	4
Age of recruitment [3]					
	5			4	2
Incidence of missed breeding					
	-			-	-
Dispersal					
Natal [4]	0.657			2	2
Adult [4]	0.010			4	2

[1]Frederiksen & Petersen 1999a; [2]Mavor *et al* 2008; [3]Frederiksen 1998; [4]Frederiksen & Petersen 1999b.

Recommended demographic rates
Estimating the survival rates of black guillemots is complicated by nests occurring in hard to reach locations, such as small rocky islands, low-lying rocky coasts, and rock crevices. The UK estimates of survival are relatively old and based on short time series (1-2 years; Ewins 1988, 1989). More recent estimates are from Iceland. The population trajectory of black guillemots in Iceland between 1977 and 1991 was similar to the present UK trend; stable (Frederiksen & Petersen 2000; JNCC 2014). There are not sufficient data to explore regional variation in age-specific survival rates, therefore population models based on these values will have to assume that the reported estimates from Iceland are representative more broadly (see accompanying material for black guillemot). In Iceland, the survival rate of black guillemot are best described in two age classes; juvenile and birds from age one onwards.

Regional differences in productivity rates have not been investigated for this species (e.g. Cook & Robinson 2010). Consequently, it may be more suitable to use colony-specific rates of productivity to parameterise population models on this species (Table 31). Long-term productivity is given for six localities in the UK by Mavor *et al* (2008).

Although published information on the age of recruitment for the black guillemot is not based on UK data (Frederiksen 1999), the corresponding population trend for this estimate was similar to the present UK trajectory. There is no information available on the incidence of

missed breeding. It may be appropriate to use estimates based on common guillemot or puffin (Table 29 and Table 32), however further matching of local population trends is recommended in order to assess suitability. Dispersal of breeding adults is low (Preston 1968; Asbirk 1979; Frederiksen & Petersen 1999b) but natal dispersal is thought to be high (Frederiksen & Petersen 1999b, 2000). The dispersal rates in Table 31 are from the multi-colony study by Frederiksen and Petersen (1999b). High levels of natal dispersal will strongly influence the subsequent population trajectory, and requires consideration when building population models for this species.

Population trend in UK
The black guillemot is largely restricted to the north and west coasts of Scotland and the coast of Ireland. Colonies in the UK increased slightly between 1982 and 2002, and are now considered to be relatively stable (JNCC 2014). However, there are regional differences in population trends (Mavor *et al* 2008; Shaw *et al* 2010).

Factors influencing survival rates
Local survival rates decrease following an increase in fishing effort (Frederiksen & Petersen 1999a).

Factors influencing productivity rates
Local productivity rates have been linked to nest quality (Ewins 1989).

Knowledge gaps
The survival rates of the UK population are poorly resolved, and information on the incidence of missed breeding is lacking. Intensive efforts at the breeding grounds would be needed to estimate these parameters.

5.10.4. Atlantic puffin (*Fratercula arctica*)

Table 32. Recommended estimates of demographic rates for Atlantic puffin.

Demographic parameter	Mean	SD$_p$	SE$_e$	Data quality	Data representation
Age-specific survival					
Immature survival (0-3 years) [1]	0.709		0.022	6	1
Immature survival (3-4 years) [1]	0.760		0.019	6	1
Immature survival (4-5 years) [1]	0.805		0.017	6	1
Adult survival ($\geq$6 year) [2-4]	0.906	0.083		6	5
Colony-specific productivity					
Fair Isle [5]	0.570	0.141		6	5
Farne Islands [6]	0.415	0.219		6	4
Isle of May [7]	0.642	0.135		6	5
Skomer [6]	0.870	0.028		6	4
St Kilda [6]	0.785	0.078		6	4
National-average productivity [4-9]					
	0.617	0.151		6	5
Age of recruitment [8,10]					
	5			6	3
Incidence of missed breeding [8]					
	0.078			4	3
Dispersal					
Natal [10]	0.230			4	2
Adult [1,8,11]	0.042	0.040		6	3

[1]Breton *et al* 2006; [2]Harris *et al* 2005; [3]Lahoz-Monfort *et al* 2011; [4]Taylor *et al* 2010; [5]Shaw *et al* 2010; [6]Mavor *et al* 2008; [7]Newell *et al* 2010; [8]Ashcroft 1979; [9]Harris 1980; [10]Harris 1983; [11]Kress & Nettleship 1988.

Recommended demographic rates
The UK estimates of survival for Atlantic puffin are largely limited to the Isle of May, Fair Isle and Skomer. A number of studies have examined these data over different time scales (see accompanying material for Atlantic puffin). Harris *et al* (2005) demonstrated that the survival rates of puffins were highly similar across different colonies. Therefore, if may be sufficient to employ a national average for survival when parameterising population models of Atlantic puffin. The estimate of adult survival in Table 32 combined the most recent colony-specific studies. Estimates of adult survival from outside of the UK also appear to be similar (Harris *et al* 2005; Breton *et al* 2006; see accompanying material for Atlantic puffin). The UK estimates of juvenile and immature survival rates are limited to relatively old mark-recapture studies based on return rates only (Harris 1983; Harris & Rothery 1985). National census data indicate that the trajectory of the UK population has changed since these studies. Furthermore, these estimates are based on data collected before the introduction of hard rings and therefore are likely to be biased by ring-loss. The values of immature survival given in Table 32 are from a recent mark-recapture study on Atlantic puffins from Canada (Breton *et al* 2006). It was not possible to verify the corresponding population trend for this estimate, and therefore caution should be applied when using these estimates to model current UK population trends.

Regional trends in productivity rates have not been investigated for this species (e.g. Cook & Robinson 2010). Consequently, it may be more suitable to use colony-specific rates of productivity to parameterise population models on this species (Table 32). The productivity of Atlantic puffin is monitored annually at three SMP Key Sites: Isle of May, Skomer and Fair Isle, and long-term productivity estimates are given for two additional UK localities by Mavor *et al* (2008).

Published information on the age of recruitment for Atlantic puffin is relatively old. The national population trend is thought to have changed since their publication (Ashcroft 1979; Harris 1984; JNCC 2014); however the reported age is similar to the estimates identified for the other species of auk considered (Tables 29-32). The majority of birds breed for the first time at age 4, but rates of productivity are usually lower than at age 5 (Ashcroft 1979; Harris 1984). Adult breeding dispersal is thought to be low (Ashcroft 1979; Harris 1983; Kress & Nettleship 1988; Breton *et al* 2006) and natal dispersal is thought to be high (Harris 1983; Breton *et al* 2006). To represent the range of dispersal rates, the values given in Table 32 are estimated from all of the listed studies (see accompanying material for Atlantic puffin). Published estimates of the incidence of missed breeding are based on short time series (3 years; Ashcroft 1979) and are therefore unlikely to be representative more broadly.

Population trend in UK
The puffin is the second most abundant seabird breeding in the UK. Population trend information is based on long-term monitoring of burrow densities on St Kilda, the Shiant Islands, the Isle of May and the Shetlands. Numbers were stable between the early 1970s and late 1980s (Lloyd *et al* 2001), with the exception of the Isle of May where there was an annual increase of 22% between 1973 and 1981 that was partially attributed to immigration (Harris & Rothery 1985). Overall, the UK population is thought to have increased between 1969 and 2002 (JNCC 2014).

Factors influencing survival rates
There is no evidence that local survival from fledging to first breeding is dependent on fledging mass or fledging date (Harris & Rothery 1985). Local survival rates of adults decrease at high population densities (Breton *et al* 2006), and due to predation by great black-backed gulls (Harris & Rothery 1985). Survival rates are also negatively influenced by a decrease in prey biomass and availability (Harris & Bailey 1992; Harris *et al* 2000a). The influence of sea surface temperatures and the Northern Atlantic Oscillation varied between colonies (Harris *et al* 2005), and survival rates do not appear to differ between the sexes (Harris *et al* 2000a).

Factors influencing productivity rates
Local productivity rates have been linked to parental age and disturbance from other burrowing animals (Ashcroft 1979), predation, nesting density (Harris 1980), prey abundance (Regehr & Rodway 1999) and levels of kleptoparasitism (Finney *et al* 2001). Outside of the UK, local productivity rates decline due to increased rainfall flooding burrows (Rodway *et al* 1998).

Knowledge gaps
The incidence of missed breeding would also benefit from further analysis across a longer time series. High levels of natal dispersal will make estimates of juvenile and immature survival difficult to deduce without multi-colony studies.

6.   Summary of demographic rates available

Table 33. National estimates of each demographic parameter by species.

Estimates are weighted means of the available demographic data, and focused to the UK where possible. Where sufficient data could not be gathered using UK examples studies from outside of the UK have been included. Estimates are colour coded to reflect an overall score associated with the data quality and data representation as follows: Red=Low (poor [0-2] quality score and poor [0-2] or good [3-6] representation score); Orange=Intermediate (Intermediate [3-4] or good [5-6] quality score and poor [0-2] representation score; OR Intermediate [3-4] quality score and good [3-6] representation score); Green=High (good quality score 5-6 and good representation score 3-6). The itemisation of these scores is detailed on the second worksheet of the accompanying material for each species. Entries based on more than one study site are highlighted in bold, and estimates of total survival from fledging to recruitment are marked with *. If a species is thought to experience survival rates similar to an adult before age 5, the intermediate boxes are shaded grey.

Common name	Survival							Productivity	Age of recruit-ment	Missed breeding	Dispersal	
	Juv.	Imm. (1-2)	Imm. (2-3)	Imm. (3-4)	Imm. (4-5)	Imm. (5-8)	Adult				Natal	Adult
Greater scaup	0.400						0.810	0.570	2			
Common eider	0.200						**0.886**	**0.379**	**3**	0.200		0.012
Goldeneye							0.770	0.365	3			**0.564**
Long-tailed duck							**0.730**	1.900	2			
Common scoter	0.749						0.783	1.838	3			0.123
Velvet scoter							0.773	0.350	2			0.688
Red-throated diver	0.600	0.620					**0.840**	**0.571**	3			0.250
Black-throated diver	0.400						**0.817**	**0.425**	5			
Great northern diver	*	*	0.770				**0.870**	**0.543**	6	0.307	0.069	0.090
Manx shearwater							0.870	**0.697**	5	0.157	**Low**	**Low**
Northern fulmar	*	*	*	*	*	0.26	0.936	**0.419**	9		**0.915**	Low
Northern gannet	0.424	0.829	0.891	0.895			0.919	**0.700**	**5**			Low
Great crested grebe							**0.725**	1.275	2			
Great cormorant	**0.540**						**0.868**	1.985	**3**		**0.240**	0.123
European shag	0.513	0.737					0.858	**1.303**	2		0.049	0.010
Arctic skua	*	*	*	0.346			0.910	**0.487**	4	0.030		Low

Common name	Survival							Productivity	Age of recruit-ment	Missed breeding	Dispersal	
	Juv.	Imm. (1-2)	Imm. (2-3)	Imm. (3-4)	Imm. (4-5)	Imm. (5-8)	Adult				Natal	Adult
Great skua	0.730						**0.882**	**0.651**	7	0.089	0.015	**Low**
Black-legged kittiwake	0.790						**0.854**	**0.690**	4	0.194	0.890	0.037
Little gull							0.800		2-3			
Black-headed gull							**0.825**	**0.625**	2			0.167
Common gull	0.410	0.710					0.828	**0.543**	3		0.700	<0.030
Lesser black-backed gull	0.820						**0.885**	0.530	5	**0.337**	0.470	
Herring gull	**0.798**						**0.834**	**0.920**	5	0.350	**0.629**	
Great black-backed gull							0.930	**1.139**	5			
Sandwich tern	0.358	0.741	0.741	0.741			0.898	**0.702**	3			
Common tern	*	0.441		0.850			**0.883**	0.764	**3-4**	Low	0.070	**0.103**
Arctic tern							**0.837**	0.380	4		0.610	**0.089**
Little tern							0.800	**0.518**	2			
Common guillemot	0.560	0.792	0.917				**0.939**	0.672	6	0.079	0.580	0.007
Razorbill	*	0.630					**0.895**	0.570	5	0.030	**0.088**	**0.047**
Black guillemot	0.731						0.870	**1.298**	5		0.657	0.010
Atlantic Puffin	*	*	0.709	0.760	0.805		**0.906**	**0.617**	**5**	0.078	0.230	**0.042**

The majority of the seabird species received high and intermediate data scores for adult survival rates, with the exception of little gull and great black-backed gull. Excluding the common eider, the survival rates of the sea duck species were less well resolved, especially for the juvenile and immature age class. The juvenile and immature survival rates for great northern diver, northern fulmar, Arctic skua, common tern, razorbill and Atlantic puffin were only available as return rates between fledging and recruitment. Juvenile and immature survival rates were not available for goldeneye, long-tailed duck, velvet scoter, Manx shearwater, little gull, black-headed gull, great black-backed gull, Arctic tern and little tern. For a number of species regional differences in population trends could not be wholly attributed to local differences in productivity (Cook & Robinson 2010). In these cases it may be important to consider regional variation in recruitment or survival rates when parameterising population models. To investigate regional differences in survival rates would require long-term mark-recapture studies from several colonies (as recommended by Robinson & Baillie 2012); alternatively this could be explored by delineating non-breeding season populations (e.g. Furness 2015).

For all of the seabird species, with the exception of little gull, there was good information on productivity. In contrast, the productivity rates of the sea duck species were less well resolved. An estimate for the modal age of recruitment was available for all of the species considered, although the variability between individuals was less well resolved. The majority of these estimates received a high or intermediate data score, with the exception of long-tailed duck, velvet scoter, Manx shearwater, great crested grebe, great skua, Sandwich tern and little tern. However, many of the reported estimates are from relatively old studies and in a number of cases national census data indicate that the trajectory of the UK population has changed since their publication. It will be important to consider any temporal or regional differences in population trend as caveats of population models that are developed using the reported values. For the majority of species there is considerably less information on the incidence of missed breeding and breeding dispersal. These variables are likely to vary markedly between colonies, depending on local population trend and resource availability. Elevated rates of natal dispersal were identified in northern fulmar, black-legged kittiwake, common gull, lesser black-backed gull, herring gull, arctic tern, common guillemot and black guillemot. This process is likely to influence the reliability of population models if it is not considered.

7. Review of density dependence in seabirds

Demographic processes such as growth, survival, productivity and recruitment are density-dependent if their rates change as a function of the density or number of individuals in a population. Density-dependent processes are said to be compensatory if they stabilise the population around the long-term average, i.e. they reduce the rate of population growth as numbers rise and increase the rate as numbers fall (Lack 1954). This negative feedback on population size is important to management because it operates to offset the losses of individuals from the population, for example, a lowered population density may cause a temporary increase in survival or productivity in the remaining individuals, supporting an increase in the population size back towards the long-term average. However, density-dependent processes may also be depensatory, slowing the rate of population growth at lower population densities. This positive feedback on population size is especially important for depleted populations and endangered species, because it acts to accelerate further population decline and can delay recovery. The expression of these opposing processes in a population may also change in relation to population size, for example a population can be depensatory at low population levels and exactly compensating at higher population levels. This mechanism may result in an optimal population density, where survival and productivity rates decrease at high and low densities (Figure 1, Allee 1931, 1938), as documented in herring gull (Parsons 1976) and common tern (Becker & Finck 1986; Sudmann 1998).

In terms of population modelling, these effects can be captured by making the demographic parameters functions of population density. Consequently, the resulting frameworks are nonlinear because populations can no longer grow exponentially. At the time of publication, the majority of population models used to assess the potential impacts of wind farms on seabirds did not consider density dependent mechanisms. Existing models have included a density-dependent adjustment on juvenile survival rates because this will also capture any associated changes in natal dispersal and recruitment (e.g. Freeman *et al* 2014). However, the contexts for including density-dependent mechanisms in population models are not well understood. This review consolidates the empirical evidence of compensatory and depensatory regulation in seabirds and sea ducks. The focus is primarily on the species considered in the individual species accounts listed in Section B, but also includes studies on similar species.

7.1. Empirical evidence of density-dependence

Depensation
Depensation is typically exhibited in populations that have been significantly depleted in size. The underlying mechanism is related to benefits associated with conspecific presence such as: anti-predator vigilance or aggression; cooperative feeding or resource defence; social thermoregulation; collective improvement of the environment; increased availability of mates; nonspecific enhancement of reproduction; and reduction of inbreeding, genetic drift, or loss of integrity by hybridisation (Stephens *et al* 1999). The majority of empirical examples of depensation in seabirds relate to anti-predator vigilance (or colonial defence) increasing rates of productivity. We identified this relationship in 14 studies that considered eight different species of seabird and sea duck (Table 34; Table 35). However, there were also twelve studies that did not identify a relationship between productivity and colony size (Table 34; Table 35). Therefore, the presence of depensation is likely to be context dependent, for example anti-predator vigilance will only be important if a population is influenced by predation (Ryder & Ryder 1981; Harris & Wanless 1988). For species and populations that are influenced by depensation, the influence of colonial defence is likely to select for higher levels of breeding synchrony in order to align colonial nest defence with specific points in the breeding season (e.g. Patterson 1965). Depensation is likely to follow a similar function shape to the Allee effect (Figure 1).
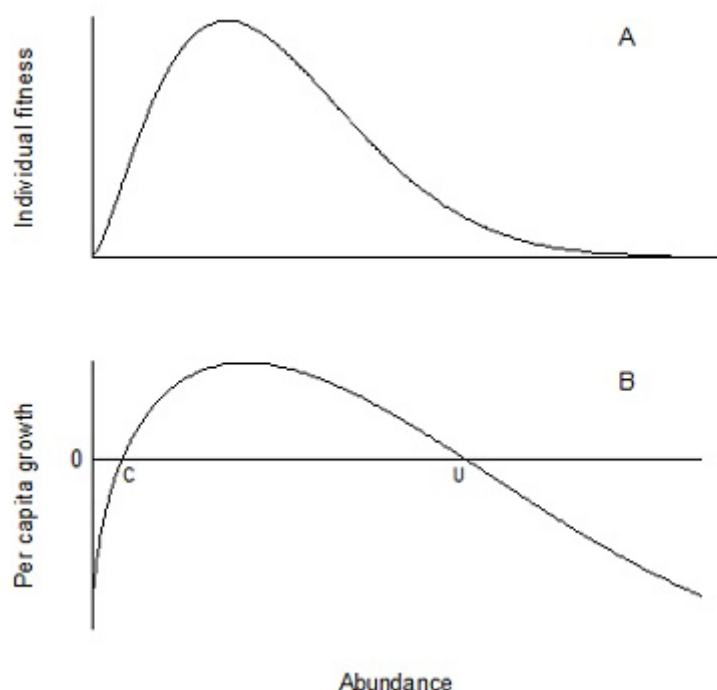
Figure 1. The Allee effect (replotted from Stephens *et al* 1999). A. At low densities, the benefits from the addition of each successive individual outweigh the costs, such that there is a net gain in individual fitness, and fitness is highest at intermediate numbers or densities. B. In this case, population growth rate may also be low at low levels of abundance, resulting in two equilibria, a lower unstable equilibrium (C) and an upper, stable equilibrium (U).

Compensation

Compensation is characterised by demographic changes that stabilise the population around the long-term average. We identified nine studies on five different species of seabirds and sea ducks that demonstrated a decrease in colony growth rates as a colony increases in size (Table 34; Table 35). For example, Porter and Coulson (1987) found the growth of a kittiwake colony to be limited by the number of attractive sites in the dense centre (also see Coulson 1983). Similarly, Chabrzyk and Coulson (1976) found that herring gulls have greater difficulty establishing a territory in a dense colony (also see Duncan 1978; Coulson *et al* 1982; Raven & Coulson 1997). Coulson and Wooller (1976) attributed this relationship to reduced survival rates. A decrease in survival rates associated with an increase in colony size was identified in seven species of seabird and sea duck across eight studies (Table 34; Table 35). However, the influence of density-dependent regulation on survival rates can also be age-specific, such that juvenile birds are more impacted by limited resources than birds older than age one (Marvelde *et al* 2009). An alternative explanation is that chicks fledge from denser colonies at significantly lighter weights (Gaston *et al* 1983). Other studies indicate that density-independent factors may have a stronger impact on survival rates at higher colony densities (Frederiksen & Bregnballe 2000b; Barbraud & Weimerskirch 2003). Here, a saturation of high quality wintering habitat may force some birds to winter in less good habitat where they are more vulnerable to poor environmental conditions. A decrease in population growth rate as the number of individuals increased can also be attributed to reduced productivity rates. This relationship was identified in seven species of seabird and sea duck across eight studies (Table 34; Table 35). In eiders this relationship was attributed to increased transmission of disease (Pöysä & Pöysä 2002) and a decrease in clutch size (Coulson 1984, 1999). In the other identified studies, this relationship was attributed to elevated disturbance from non-breeding conspecifics and predation of eggs and chicks by neighbouring pairs. However, there are also twelve studies that did not identify a relationship between productivity and colony size (Table 34; Table 35). This result may reflect a colony

that is not limited by resources. Alternatively it may indicate that density-dependence operates through variation in recruitment or immigration.
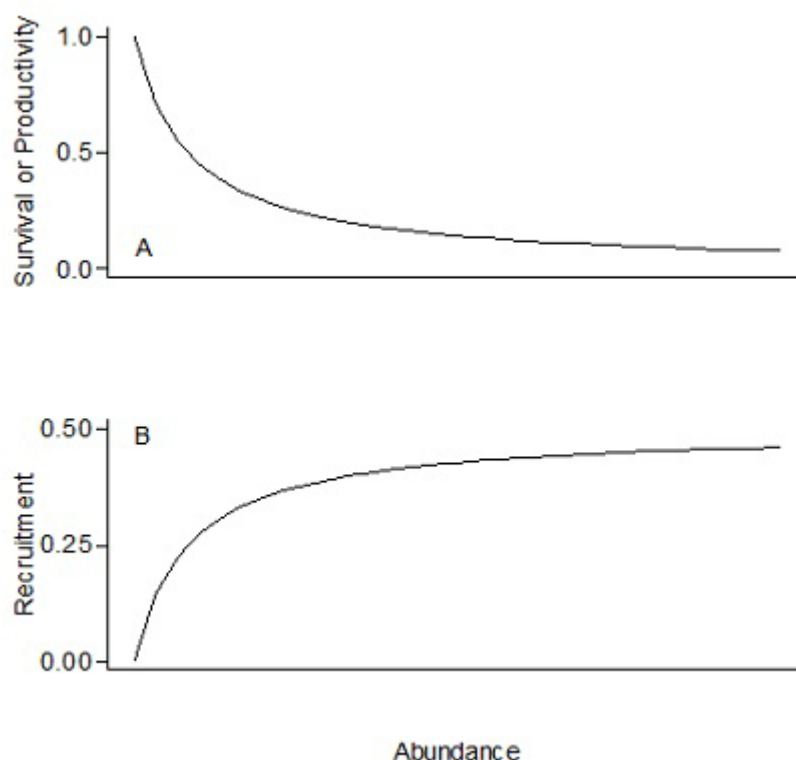
Figure 2. The compensatory (Beverton-Holt function) effect. A. At high population densities, increasing competition and depletion of resources will often result in decreased survival or productivity rates. B. Recruitment increases as the survival or productivity rates decrease resulting in a population in equilibrium (compensatory).

Elevated mortality rates in the breeding population may not influence the total colony size because new recruits take over high quality nesting sites left vacant, and thus achieve productivity rates that are more similar to experienced birds (e.g. Coulson 1971). Here, any changes in survival are exactly offset by a change in recruitment or immigration (Fig. 2; Beverton-Holt function; Beverton & Holt 1957). This process can be identified by quantifying the age of recruitment, the proportion of non-breeding individuals in the population and the rates of immigration and emigration. An increase in the age of recruitment following a decrease in resource availability (such as nesting sites) was identified in nine species (Table 34). Similarly, an increase in recruitment from the non-breeding pool of adults in response to an increase in resource availability was identified in five species (Table 34). Finally, an increase in emigration in response to a decrease in resource availability was identified in four species, and an increase in immigration in response to an increase in resource availability was identified in six species. There were also three studies that did not report a relationship between colony size and the proportion of adults in the non-breeding pool (Table 34; Table 35). These studies considered colonies that were increasing at the time of publication. Consequently, the pool of non-breeding adults may have already been exhausted, and thus colony growth was predominantly driven by immigration.

7.2. Potential impacts from offshore wind farm developments

Wind farm developments act in a density-independent manner, i.e. they may affect a proportion of the population regardless of its size. This section offers a brief evaluation of the potential density-dependent processes that a seabird colony may experience in response to offshore wind farm developments.

Reduced survival

In the short term, any elevated rates of mortality may not manifest in the size of the breeding population. This is because any relative increase in resource availability, such as high quality nesting sites (caused by death of one or both of the breeding pair occupying them) will be offset by an increase in productivity, a decrease in the age of recruitment, an increase in the recruitment of individuals from the non-breeding pool or an increase in immigration. However, once these mechanisms have become saturated (i.e. there are no more individuals in the non-breeding pool) a change in the population size is likely to result. In colonies that experience depensatory regulation, this has the potential to be highly destabilising.

Reduced productivity

Seabirds and sea ducks often increase their breeding dispersal in response to failed breeding (e.g. Boulinier *et al* 2008; Dow & Fredga 1983; Perrins & Smith 2000). If wind farm developments decrease rates of productivity (e.g. through displacement of foraging birds, Drewitt & Langston 2006), this may also drive changes in local emigration rates and lead to further reductions in the colony size as birds redistribute. The continued level of disturbance from the offshore development may also prevent colonies from being compensated by elevated levels of immigration or recruitment. This may be especially pertinent to colonies that are within designated Special Protection Areas, where there is a commitment to protect selected colonies.

Conclusions and future directions

This review of density-dependent regulation in seabirds and sea ducks identifies a large number of studies that report compensatory mechanisms to influence rates of productivity, survival, recruitment and dispersal. However, the review highlights that there is not a simple mechanism of density-dependence that can be applied uncritically in all situations. Rather the influence of density-dependence relates to a complex interaction between resource availability, colony size and other local factors, such as predation. The dynamics of a colony should be evaluated if density-dependence is to be realistically incorporated within population models that evaluate the impacts of wind farm developments. The identification of compensation was most prevalent in studies that examined rates of recruitment. This means that per capita growth rates will be higher at low colony densities, and in terms of population modelling, recovery will be quicker if compensatory processes are considered. Thus, in many cases adopting a density-independent modelling framework will overestimate potential impacts. However, in certain species and populations there was also clear evidence that depensatory mechanisms operate on rates of productivity. Here, density-independent models will underestimate potential impacts. Depensatory regulation of productivity rates was reported in almost twice the number of studies that reported compensatory regulation of this demographic parameter, albeit across a similar number of species (Table 35). The ability of compensatory density-dependent mechanisms to support population recovery may largely depend on the demographic rate impacted, and whether the severity of the impact changes over time (e.g. through habituation). Further modelling of compensatory and depensatory functions on different demographic rates is recommended in order to elucidate their influence on the resulting population size.

Table 34. Studies assessing the effect of population density or population size on seabird demography.

Species	Density-dependent process	Demographic process	Effect	Reference
Great cormorant	Compensation	Age of recruitment	Yes	Frederiksen & Bregnballe 2000a
European shag	Compensation	Age of recruitment	Yes	Swann & Ramsay 1983b, cited Swann & Ramsay 1983a
Black-headed gull	Compensation	Age of recruitment	Yes	Lebreton *et al* 1990
Black-legged kittiwake	Compensation	Age of recruitment	Yes	Porter & Coulson 1987
Herring gull	Compensation	Age of recruitment	Yes	Duncan 1981; Chabrzyk & Coulson 1976; Coulson *et al* 1982
Audouin's gull	Compensation	Age of recruitment	Yes	Oro & Pradel 2000
Common guillemot	Compensation	Age of recruitment	Yes	Swann & Ramsay 1983a
Razorbill	Compensation	Age of recruitment	Yes	NERC 1977, cited Swann & Ramsay 1983a
Atlantic puffin	Compensation	Age of recruitment	Yes	Harris 1983; Kress & Nettleship 1988
Great cormorant	Compensation	Emigration	Yes	Frederiksen & Bregnballe 2000a
Common guillemot	Compensation	Emigration	Yes	Crespin *et al* 2006b
Northern gannet	Compensation	Emigration and Immigration	Yes	Murray & Wanless 1997; Moss *et al* 2002
Great skua	Compensation	Emigration and Immigration	Yes	Phillips *et al* 1999b; Meek *et al* 2011
Great cormorant	Compensation	Immigration	Yes	Hénaux *et al* 2007
European shag	Compensation	Immigration	Yes	Aebischer 1995
Herring gull	Compensation	Immigration	Yes	Chabrzyk & Coulson 1976; Duncan 1978; Coulson *et al* 1982
Atlantic puffin	Compensation	Immigration	Yes	Harris 1983
Common eider	Compensation	Incidence of missed breeding	Yes	Coulson 1984

Species	Density-dependent process	Demographic process	Effect	Reference
Common eider	Compensation	Incidence of missed breeding	Yes	Coulson 1984
Goldeneye	Compensation	Incidence of missed breeding	Yes	Eriksson 1979
Northern fulmar	Compensation	Incidence of missed breeding	No	Ollason & Dunnet 1983
Great skua	Compensation	Incidence of missed breeding	Yes	Hamer *et al* 1991
Lesser black-backed gull	Compensation	Incidence of missed breeding	No	Calladine & Harris 1997
Herring gull	Compensation	Incidence of missed breeding	No	Calladine & Harris 1997
Arctic tern	Compensation	Incidence of missed breeding	Yes	Monaghan *et al* 1992
Great northern diver	Compensation	Population growth	Yes	Grear *et al* 2009
Velvet scoter	Compensation	Population growth	Yes	Hartman *et al* 2013
Northern gannet	Compensation	Population growth	Yes	Lewis *et al* 2001
Black legged kittiwake	Compensation	Population growth	Yes	Coulson 1983; Porter & Coulson 1987
Herring gull	Compensation	Population growth	Yes	Chabrzyk & Coulson 1976; Duncan 1978; Coulson *et al* 1982; Raven & Coulson 1997
Great northern diver	Compensation	Productivity	Yes	Evers 2004
Common eider	Compensation	Productivity	Yes	Coulson 1984; 1999; Pöysä & Pöysä 2002
Goldeneye	Compensation	Productivity		Andersson & Eriksson 1982
Northern fulmar	Compensation	Productivity	No	Falk & Møller 1997; Lewis *et al* 2009

Species	Density-dependent process	Demographic process	Effect	Reference
Southern fulmar	Compensation	Productivity	No	Jenouvrier *et al* 2005
Northern gannet	Compensation	Productivity	No	Nelson 1966
Northern gannet	Compensation	Productivity	No	Nelson 1966
European shag	Compensation	Productivity	No	Potts *et al* 1980
Arctic skua	Compensation	Productivity	No	Jones 2003
Great skua	Compensation	Productivity	No	Hamer & Furness 1991
Great skua	Compensation	Productivity	Yes	Jones 2003
Black-legged kittiwake	Compensation	Productivity	No	Coulson 1971
Audouin's gull	Compensation	Productivity	No	Oro *et al* 1999
California gull	Compensation	Productivity	No	Pugesek & Diem 1983
Herring gull	Compensation	Productivity	Yes	Kilpi 1989
Glaucous-winged gull	Compensation	Productivity	Yes	Hunt & Hunt 1976
Great black-backed gull	Compensation	Productivity	Yes	Butler & Trivelpiece 1981
European shag	Compensation	Recruitment from non-breeding population	Yes	Potts *et al* 1980
Great skua	Compensation	Recruitment from non-breeding population	Yes	Klomp & Furness 1992b
Black legged kittiwake	Compensation	Recruitment from non-breeding population	Yes	Porter & Coulson 1987
Audouin's gulls	Compensation	Recruitment from non-breeding population	Yes	Tavecchia *et al* 2007
Common guillemot	Compensation	Recruitment from non-breeding population	Yes	Votier *et al* 2008
Common eider	Compensation	Survival	Yes	Milne 1974
Blue petrel	Compensation	Survival	Yes	Barbraud & Weimerskirch 2003
Great cormorant	Compensation	Survival	Yes	Frederiksen & Bregnballe 2000b

Species	Density-dependent process	Demographic process	Effect	Reference
Black-legged kittiwake	Compensation	Survival	Yes	Coulson & Wooller 1976; Coulson 2001
Mediterranean gull	Compensation	Survival	Yes	Marvelde *et al* 2009
Common guillemot	Compensation	Survival	Yes	Crespin 2006b
Atlantic puffin	Compensation	Survival	Yes	Harris & Wanless 1991; Breton *et al* 2006
Atlantic puffin	Compensation	Survival	Yes	Harris & Wanless 1991; Breton *et al* 2006
Arctic skua	Depensation	Productivity	Yes	Phillips *et al* 1998
Black-legged kittiwake	Depensation	Productivity	Yes	Coulson & White 1958; Porter 1990; Falk & Møller 1997; Frederiksen *et al* 2004a
Black-headed gulls	Depensation	Productivity	Yes	Patterson 1965
Sandwich terns	Depensation	Productivity	No	Veen 1997
Common terns	Depensation	Productivity	Yes	Becker 1995; Hernández-Matías *et al* 2003
Common guillemot	Depensation	Productivity	Yes	Birkhead 1977
Common guillemot	Depensation	Productivity	No	Harris & Wanless 1988
Atlantic puffin	Depensation	Productivity	Yes	Harris 1980
Herring gull	Depensation/ Compensation	Productivity	Yes	Parsons 1976
Common tern	Depensation/ Compensation	Productivity	Yes	Becker & Finck 1986; Sudmann 1998

Table 35. Studies assessing the effect of population density or population size on seabird demography. Numbers detail the number of studies identified.

Demographic rate	Density-dependent mechanism	Divers and grebe	Sea ducks	Procellariiformes	Gannet	Cormorants	Skuas	Large gulls	Small gulls	Terns	Auks	Total
Population growth	Compensation	1	1		1			4	2			**9**
	Absent											**0**
Productivity	Depensation						1	1	6	4	2	**14**
	Compensation	1	3					1	3			**8**
	Absent			3	1	1	2	1	2	1	1	**12**
Survival	Compensation		1	1		1			2		3	**8**
	Absent											**0**
Recruitment	Compensation		2			2	1	4	2	1	4	**16**
	Absent			1				2				**3**
Dispersal	Compensation				2	3	2	3			2	**12**
	Absent											**0**

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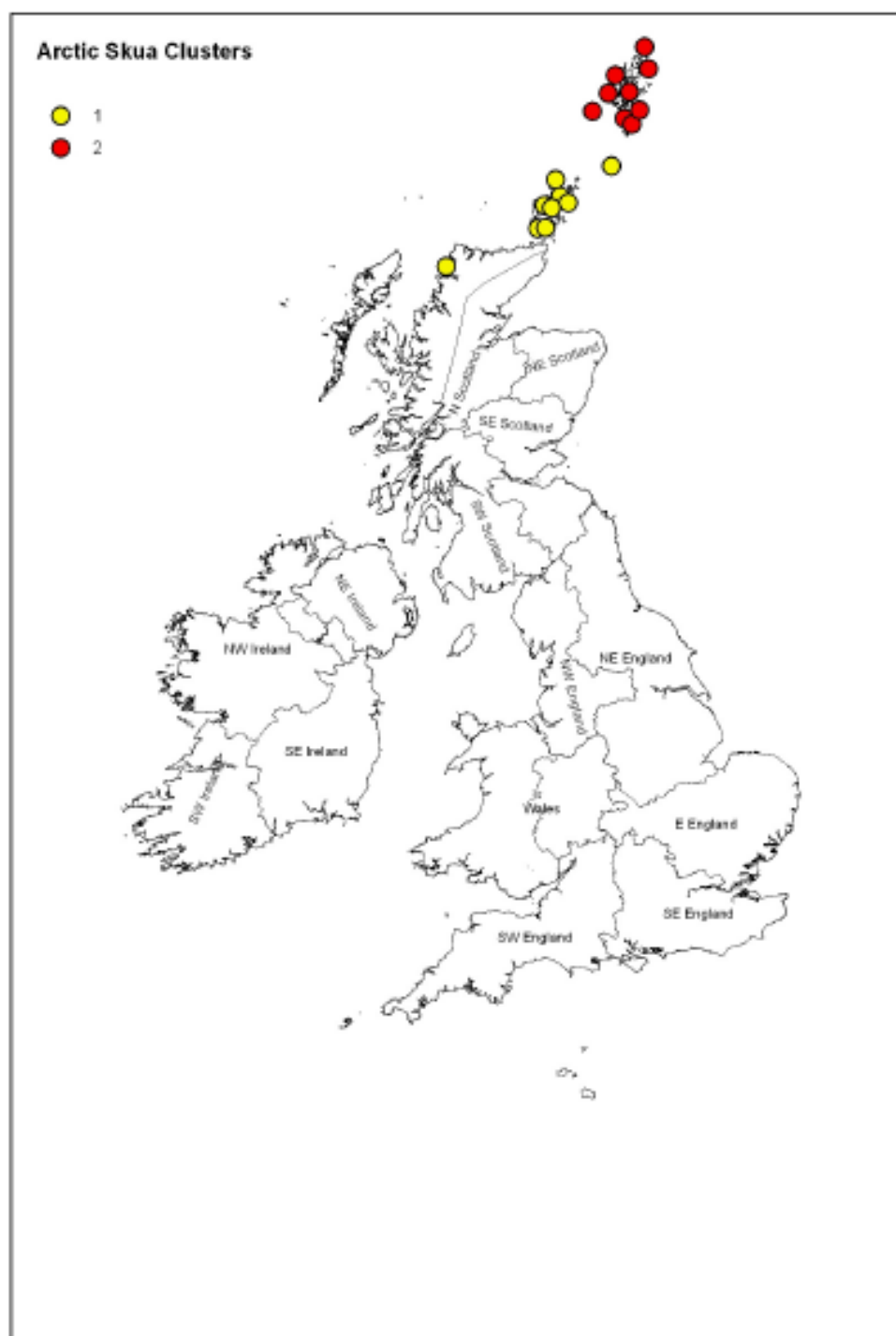
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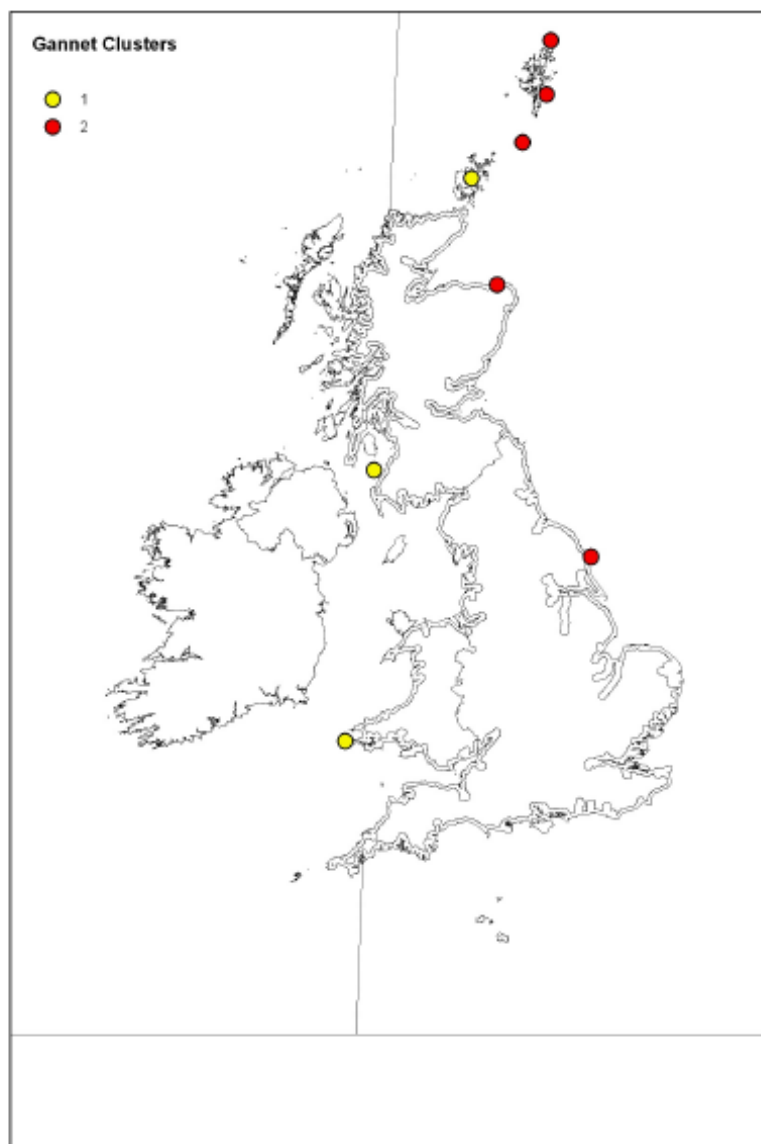
S1. Colony membership of clusters based on analysis of northern gannet breeding success data, overlaid with existing OSPAR monitoring regions (taken from Cook & Robinson 2010). The West Coast cluster is broadly contiguous with the Celtic Sea OSPAR region, with the addition of Orkney, and the East Coast Cluster is broadly contiguous with the Greater North Sea OSPAR region. The West Coast cluster encompasses the North West England and Isle of Man, North West Scotland, Orkney, South West Scotland, Wales, South West Ireland and South East Ireland SMP regions, as well as regional seas 4, 5, 6 and part of 7. The East Coast Cluster encompasses the East England, North East England, South East Scotland, North East England and Shetland SMP regions as well as Regional Seas 1, 2 and part of 7.
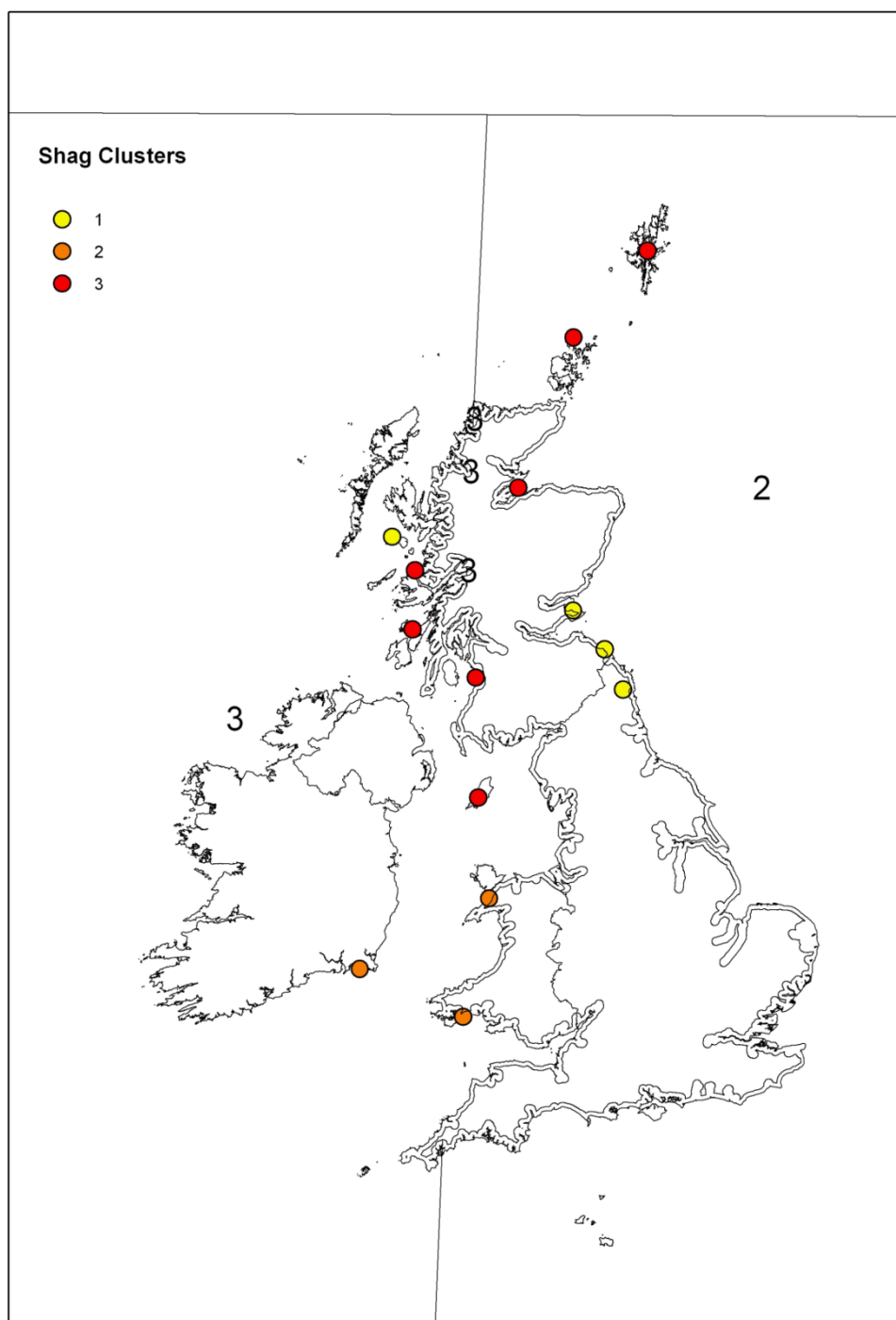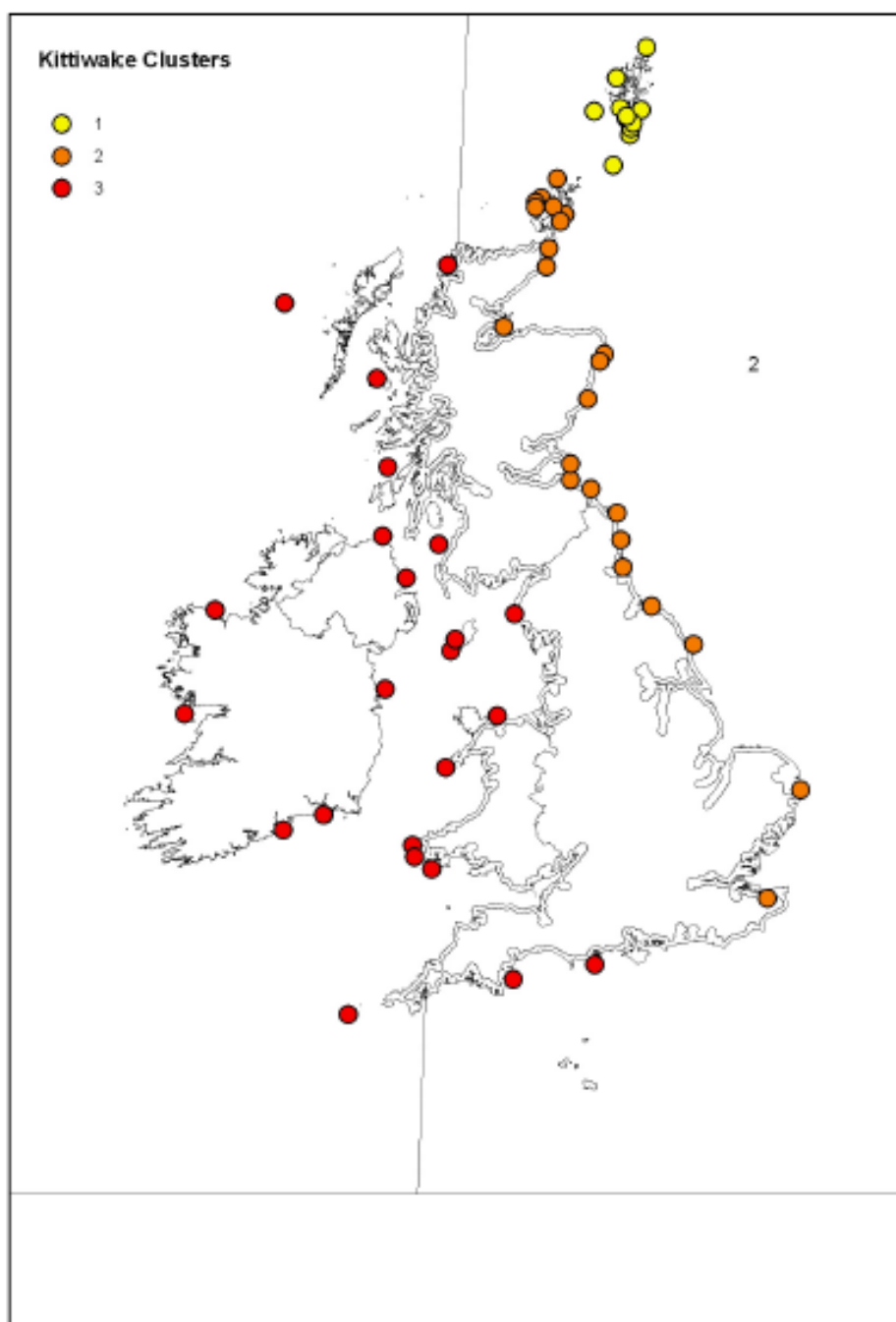
S2. Colony membership of clusters based on analysis of European shag breeding success data, overlaid with existing OSPAR monitoring regions (taken from Cook & Robinson 2010). The East Coast of Scotland and Orkney and the Shetland clusters are within the Greater North Sea OSPAR Region and the West Coast of England and Wales cluster is within the Celtic Sea (Cook & Robinson 2010).
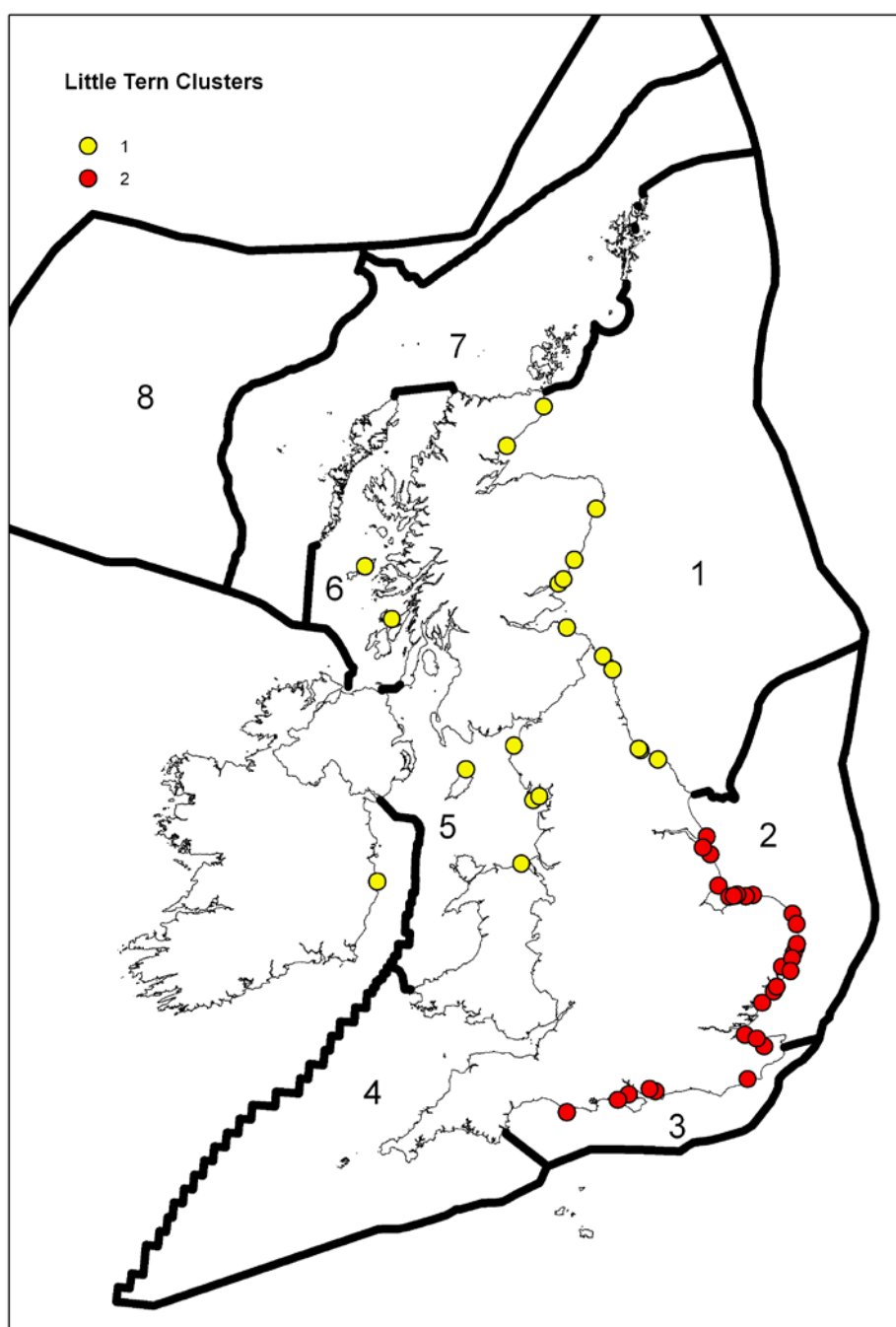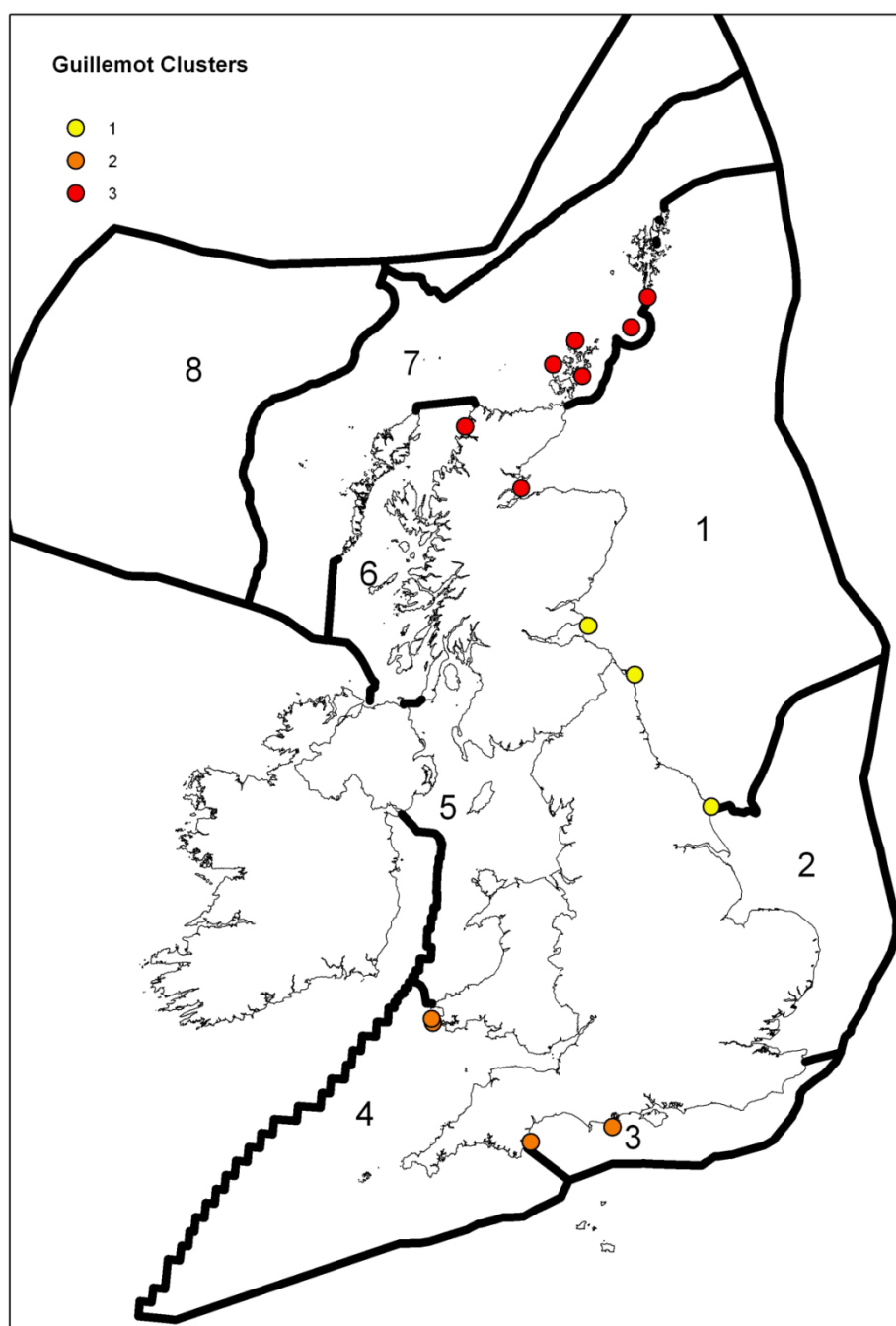
S3. Colony membership of clusters based on analysis Arctic skua breeding success data, overlaid with existing Regional Seas monitoring regions (taken from Cook & Robinson 2010). The Shetland Cluster is within the Greater North Sea OSPAR region and Regional Seas 7. It is contiguous with the Shetland SMP region. The Orkney and North Scotland cluster is split between the Celtic Sea and Greater North Sea OSPAR regions and Regional Seas 6 and 7. It encompasses the North West Scotland and Orkney SMP regions.
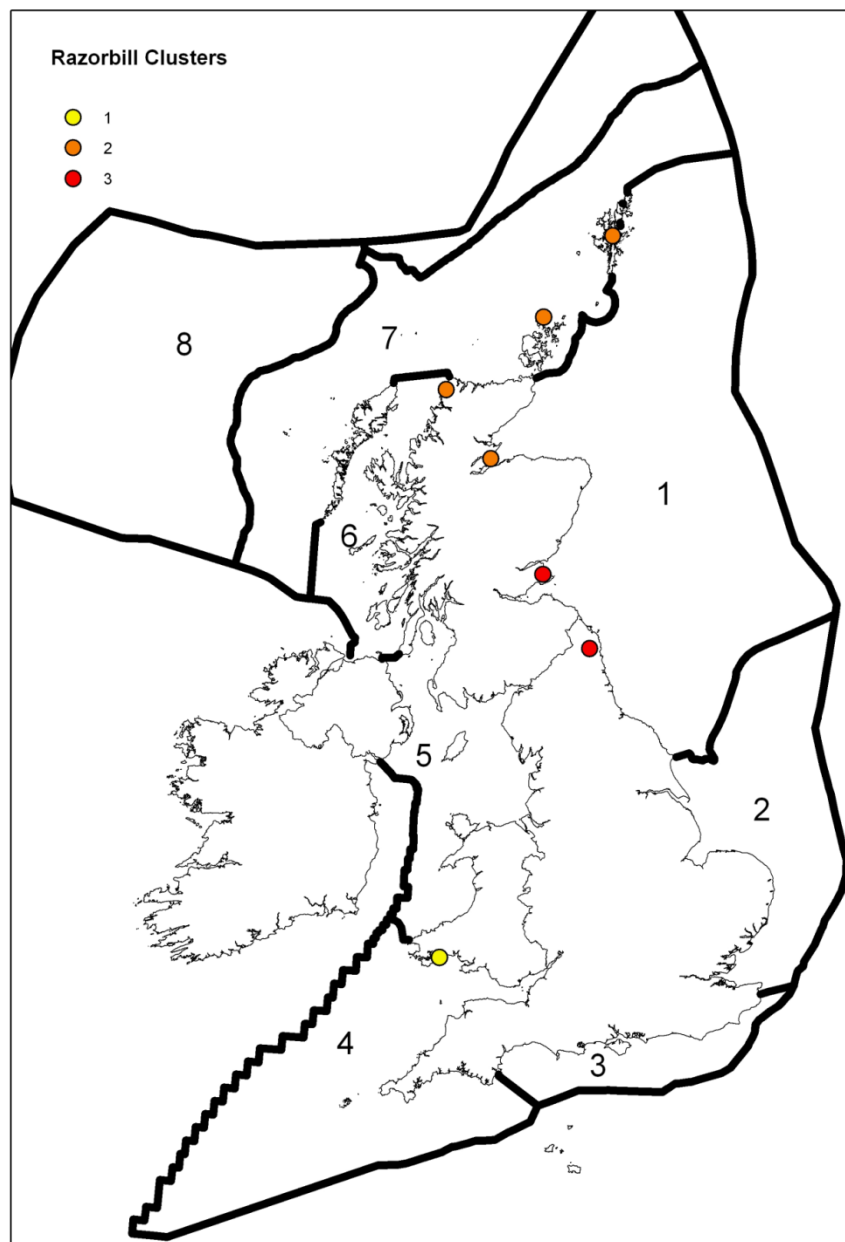
S4. Colony membership of clusters based on analysis of black-legged kittiwake breeding success data, overlaid with existing OSPAR monitoring regions (taken from Cook & Robinson 2010). The Shetland population falls within regional sea 7 and the Shetland SMP region. The Eastern population encompasses regional seas 1, 2 and 3 and parts of regional seas 4 and 7 as well as the South East England, East England, North East England and North East Scotland SMP regions and parts of the North Scotland and South West England SMP Regions. The Western population encompasses regional seas 5 and 6 and parts of regional seas 4 and 7 as well as the Wales, South East Ireland, North West England, South West Scotland and North West Scotland SMP regions and parts of the South West England, North Scotland and Orkney SMP regions.

S5. Colony membership of clusters based on analysis of little tern breeding success data, overlaid with existing OSPAR monitoring regions (taken from Cook & Robinson 2010). The Southern population encompasses the South West England, South East England, East England and North East England SMP (SMP) regions and Regional Seas 2, 3 and 4, all of which are experiencing declines in breeding success. The Northern population encompasses the North Scotland, North East Scotland, North West England, South East Scotland, South West Scotland, Wales and South East Ireland SMP regions and Regional Seas 1, 5, and 6, in which breeding success remains relatively stable.

S6. Colony membership of clusters based on analysis common guillemot breeding success data, overlaid with existing Regional Seas monitoring regions (taken from Cook & Robinson 2010). The North of Scotland group encompasses regional seas 6 and 7 and part of regional sea 1 and the North Scotland, North West Scotland, Orkney and Shetland SMP regions. The East coast group encompasses regional sea 2 and part of regional sea 1 and the South East Scotland and North East England SMP regions. The South West group encompasses regional seas 3, 4 and 5 and the South West England and Wales SMP regions.

S7. Colony membership of clusters based on analysis razorbill breeding success data, overlaid with existing regional seas monitoring regions. The North Scotland, Orkney and Shetland cluster is split between the Greater North Sea and Celtic Sea OSPAR regions. The East Coast of Scotland cluster is within the Greater North Sea OSPAR region and the South Wales cluster is within the Celtic Sea OSPAR region. The North Scotland, Orkney and Shetland cluster is split between regional seas 1, 6 and 7 and between the North West Scotland, North Scotland, North East Scotland, Orkney and Shetland SMP regions. The East Coast of Scotland cluster is within regional sea 1 and split between the South East Scotland and North East England SMP regions. The South Wales cluster is within regional sea 4 and the Wales SMP region.