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Black-legged kittiwake population dynamics and drivers of population change in the context of offshore wind development

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Summary

This report presents a summary of existing evidence, and potential research opportunities, to better understand the population dynamics of black-legged kittiwakes and how populations might respond to potential additional mortality from offshore wind farm development. This work has been undertaken on behalf of the Offshore Wind Strategic Monitoring and Research Forum (OWSMRF) (https://jncc.gov.uk/our-work/owsmrf/). OWSMRF is an industry-led collaborative forum that aims to identify and develop research to fill critical knowledge gaps in our understanding of the impact of offshore wind development on the marine environment.

OWSMRF stakeholders identified a lack of understanding of cumulative impacts from offshore wind development on kittiwakes as one of the greatest environmental consenting risks. Improving confidence in models that assess population response to offshore wind farm mortality was identified as one of three key knowledge gaps in this area, the other two being: reducing uncertainty around estimates of collision mortality and connectivity between offshore wind farms and SPAs.

JNCC organised a workshop that aimed to identify research opportunities that will improve understanding of kittiwake population dynamics and drivers of population change in the context of offshore wind development, thereby improving our ability to predict population response to novel impacts. During the workshop, experts were invited to suggest research that would fill gaps in our current understanding of kittiwake population dynamics, under three high-level objectives:

1. Reduce uncertainty around current PVA (population viability analysis) modelling approaches through obtaining better evidence with which to parameterise PVA models;

2. Improve understanding of the wider context in which current typically colony-specific PVA approaches sit, e.g. the wider spatial scale at which population processes, such as meta-population dynamics and density dependence might be operating;

3. Identify drivers of change in kittiwake populations and their mechanism of operation to understand the relative impact of offshore wind development alongside other pressures, and options for managing pressures to inform discussions around IROPI/derogation conservation measures.

This report provides a summary of existing evidence, followed by research opportunities (RO) suggested by experts that would fill gaps in our current understanding of kittiwake population dynamics in the context of offshore wind development. The research opportunities were:

Research Opportunities leading to better parameterisation of current population modelling approaches and improved understanding of wider context of kittiwake population dynamics (Objectives 1 and 2 above):

RO3.1 Use of large-scale strategic modelling approaches to better understand kittiwake meta-population dynamics and estimate connectivity among colonies. This project makes use of an existing meta-population modelling framework, which has been developed by the University of Glasgow, to estimate the strength of connectivity among kittiwake colonies in key areas of Britain and Ireland. The outputs of this model will also inform the optimisation of future monitoring and data collection of the most influential demographic parameters. This would provide a better understanding of the wider population

context in which individual kittiwake SPA colony dynamics operate, e.g. is the Flamborough and Filey Coast SPA operating as a source or sink population and how does this change predictions of population response to additional mortality?

RO3.2 Further development of a population modelling tool that assists with assessing population response to changes in mortality or productivity. This project will add additional functionality to an existing on-line "PVA Tool", specifically a meta-population function that allows emigration and immigration to be incorporated into the population models. Movement rates will be informed by the outputs of RO3.1. This would improve confidence in predicted population response to estimated mortality from a planned offshore wind development by bringing more biological realism to current PVA approaches. It would also enable better modelling of other management measures that could increase productivity and survival, thereby informing evaluation of conservation measures.

RO3.3 Strategic mark-recapture studies to improve empirical estimates of connectivity and survival. This project will assess the feasibility of a large-scale kittiwake mark-recapture study, such as colour-ringing, in the UK to improve empirical estimates of key demographic rates such as survival and dispersal rates. Better estimates of these parameters are needed to improve the parameterisation of PVA and meta-population models, e.g. RO3.1 and RO3.2, leading to improved confidence in predictions of how kittiwake populations are likely to respond to offshore wind farm mortality.

RO3.4 Reconstructing adult survival rates for populations where empirical estimates are lacking. This project addresses the lack of population-specific empirical estimates of kittiwake survival rates. It will make use of an existing modelling approach developed by the University of Glasgow to reconstruct survival estimates for kittiwake colonies of interest where this information is lacking. This information would enable better parameterisation of population models, as described in RO3.1 and RO3.2.

RO3.5 Estimating the form and strength of compensatory density-dependence in kittiwake population dynamics at different spatial scales. This project makes use of the rich kittiwake colony monitoring datasets available in the UK, as well as existing robust population modelling approaches, to try to detect patterns of compensatory density-dependence in kittiwake colonies. The form and strength of density dependence used in PVA models strongly influences model predictions about how the population will respond to additional mortality. Obtaining and implementing novel empirical data on how density dependence operates on populations and the spatial and temporal scales over which density dependence might occur will improve confidence in PVA predictions.

RO3.6 Detecting depensation effects by modelling kittiwake population dynamics. With this project, it is proposed to build a model to assess the relative importance of depensatory density dependence in breeding kittiwake populations, evaluate its strength and infer where and when this process may be more likely to occur. Identifying at what population size/density kittiwake populations are at risk of declining to extinction due to depensation effects is important as additional mortality on populations could inadvertently push populations into such a decline.

RO3.7 Evaluating the proportion of UK kittiwake populations that are non-breeding adults. This RO is a desk-based study to estimate the extent of non-breeding in UK kittiwake populations using available data on population size, breeding success and adult survival. The results from this RO would help better estimate the proportion of non-breeders in kittiwake populations and anticipate their ability to buffer a population against declines (including steeper declines for already declining populations) in size due to reduced adult survival and/or productivity. This will bring more biological realism to current PVA models and improve confidence in predictions about how populations will respond to offshore wind mortality.

Research Opportunities focussing on understanding potential kittiwake population response to changes in management of drivers of population change (Objective 3 above):

RO3.8 Examining the ecosystem processes driving the relationship between kittiwake breeding success and sea surface temperature. This RO will improve understanding of how climate change is impacting kittiwake productivity and how other factors may be compounding the negative effects of warming seas. This RO will examine how various environmental and biological factors may have led to variation in breeding success between colonies and within colonies over time. Better understanding of what determines productivity at different colonies will improve predictions of how kittiwake populations are likely to change in the future due to climate change, along with other drivers of change such as offshore wind development. It will also ensure that potential conservation measures account for environmental and biological drivers of population change, and that conservation measures are effective and achieve the desired outcomes.

RO3.9 Kittiwake diets during the breeding season, and the relationship between prey availability and productivity. This project is a combination of desk-based and field studies to determine kittiwake dietary patterns during the breeding season and improve our understanding of the relationship between non-sandeel prey availability and productivity. This RO will help build confidence in how kittiwake populations are responding to declines in sandeel availability and thus assess their resilience to additional mortality, e.g. from offshore wind development. This would also provide key evidence to inform conservation measures, such as how kittiwake populations might respond to changes in management of commercial fisheries.

RO3.10 Assessing the current and future condition of alternative fish prey populations: a desk-based study. With this RO, it is proposed to review the literature on forage fish species, specifically population status and trends, drivers of population dynamics, current fishing pressure and projected impacts of climate change on forage fish populations. This information will assist with identifying kittiwake colonies that are vulnerable to additional mortality and those that are likely to be more resilient to additional mortality, e.g. from OWF development, due to predicted availability of prey/forage fish species. Additionally, this will help assess which conservation management measures may be ineffective due to changes in forage fish populations.

RO3.11 Quantifying the effects of fisheries management on kittiwake demography. This RO involves designing a monitoring plan that would maximise power to detect changes in demographic rates that could be attributed to changes in fisheries management. This would be followed by data collection prior to changes in fishing effort, which would provide a baseline against which to assess demographic response to management. This project will enable evaluation of the effectiveness of fishing-related conservation measures.

RO3.12 Predicting the demographic consequences of various potential measures to manage pressures on kittiwake populations. This project would develop a strategic modelling framework that would enable identification of those pressures that exert the most detrimental effects on kittiwake demographic rates and then evaluate potential management options in terms of population rates of change. This information would bring wider context to current PVA assessments of population response to offshore wind mortality and inform likely efficacy of potential conservation measures. Specifically, this project would demonstrate the relative impact of offshore wind development on kittiwake populations, alongside other drivers of population change.

Several of these research opportunities would complement each other, and combined, could greatly increase our understanding of kittiwake population dynamics and how populations are likely to respond to offshore wind farm development and conservation management measures. This would lead to significant reductions in uncertainty in assessments of cumulative impacts on kittiwake from offshore wind farm developments.

Contents

1 Background

Offshore wind farms (OWF) are seen as a key part of efforts to combat climate change (Cook *et al*. 2018; Snyder & Kaiser 2009). However, there are a number of significant concerns about the potential of these wind farms to have a negative impact on wildlife and biodiversity, particularly in relation to birds (Drewitt & Langston 2006; Gibson *et al*. 2017). To inform the planning process of the potential impacts of the effects associated with wind farms, detailed Environmental Impact Assessments (EIA) and Habitats Regulations Appraisals (HRA) are required. EIAs assess impacts to the wider environment, whilst HRAs assess whether a plan or project will have an adverse effect on a Natura 2000 site protected under either the European Commission's Habitats Directive (Directive 92/43/EEC) or Birds Directive (2009/147/EC).

As the number of wind energy developments increase globally both onshore and offshore, the potential associated environmental impacts are receiving considerable attention, particularly avian impacts. This is of particular concern at the cumulative scale, i.e. considering impacts of wind farms combined rather than of individual developments in isolation. As the scale of offshore wind farm development expands, the risk of reaching unacceptable levels of cumulative impacts increases. In order to undertake meaningful cumulative impact assessments, there is a need for improved understanding of how birds respond to offshore wind farms and how to quantify the risk to populations of concern. Without such information, decision making is necessarily precautionary, and there is a risk that offshore wind farms may not be deployed at sufficient scale to contribute fully to emission reductions targets and ambitions.

The potential impacts of wind farms on bird populations can be grouped into three main types: i) collision mortality; ii) displacement and attraction effects and; iii) barrier effects (e.g. (Cook *et al*. 2018; Vanermen *et al*. 2015). As part of the impact assessment process, the likely effects (e.g. collision and/or displacement effects) of a proposed wind farm on birds are estimated. Once the magnitude of these effects have been estimated, it is necessary to understand which SPA colonies (if any) these affected birds originate from, in order to then be able to assess the impact of these effects on the SPA population (for HRA assessments) and/or which wider population these affected birds are part of (for EIA assessments). Finally, population modelling is frequently used to evaluate the likely population response to reductions in survival or productivity predicted to occur, once the scale of effect and population linkages have been established (Cook *et al*. 2018).

1.1 OWSMRF

The Offshore Wind Strategic Monitoring and Research Forum (OWSMRF) (https://jncc.gov.uk/our-work/owsmrf/) is an industry-led collaborative forum that aims to identify and develop research to fill critical knowledge gaps in our understanding of the impact of offshore wind development on the marine environment. OWSMRF was initiated by JNCC and six offshore wind developers: EDF-Renewables, Equinor, Innogy, Ørsted, Scottish Power Renewables, and Vattenfall. The work of OWSMRF follows on from previous work looking to identify research priorities for improved understanding of ornithological issues relating to the expansion of the UK offshore wind industry, such as the Strategic Ornithological Support Services group (SOSS, https://www.bto.org/our-science/wetland-and-marine/soss) and Collaborative Offshore Wind Research into the Environment (COWRIE), and more recently, commissioned summaries of research needs e.g. (Furness 2016), the Scottish Marine Energy Research (ScotMER) evidence maps (https://www2.gov.scot/Topics/marine/marineenergy/mre/research), as well as work delivered through opportunities such as ORJIP-Offshore Wind (https://www.carbontrust.com/our-projects/orjip-offshore-wind) and the BEIS Offshore

Energy Strategic Environmental Assessment research programme (https://www.gov.uk/guidance/offshore-energy-strategic-environmental-assessment-sea-an-overview-of-the-sea-process#offshore-energy-sea-research-programme).

The OWSMRF Developer Group agreed to support an initial pilot year during which the focus was on ornithology issues. OWSMRF uses a collaborative process to identify knowledge gaps and research opportunities to fill those gaps. The process involves consulting OWSMRF Key Stakeholders: RSPB, Natural England (NE), Scottish Natural Heritage (SNH), Natural Resources Wales (NRW), Northern Ireland Environment Agency (NIEA) and Marine Scotland Science (MSS). In May 2019, Key Stakeholders were asked to identify which species and knowledge gaps they saw as currently posing the greatest uncertainty in impact assessments for offshore wind development, and most likely to lead to uncertainty in decision making around offshore wind farm consenting in the next few years. OWSMRF Key Stakeholders agreed that uncertainty around in-combination and cumulative impacts of offshore wind development on black-legged kittiwake (*Rissa tridactyla*) populations currently posed the greatest uncertainty.

Three priority knowledge gaps (KG) to inform cumulative/in-combination assessments were identified:

- KG1: reducing uncertainty around estimates of wind farm collision mortality;
- KG2: improving understanding of connectivity between OWF and SPAs;
- KG3: improving confidence in modelling population consequences of wind farm effects.

A review of the current evidence base and identification of research opportunities that would assist with reducing uncertainty around wind farm collision mortality (KG1) and would lead to more certainty about connectivity between SPAs and OWF (KG2) has already been carried out and reported:

Better estimates of collision mortality to black-legged kittiwakes at offshore wind farms (https://hub.jncc.gov.uk/assets/bbe5e9fa-0ef2-4cb7-a34a-a9c87960bb75)

Better linking effects of offshore wind farms on black-legged kittiwakes to populations (https://hub.jncc.gov.uk/assets/bdd7e6f0-b0fe-431d-b403-85a456aacdc9)

This current report describes work for KG3, obtaining a better understanding of kittiwake population dynamics and drivers of population change in the context of offshore wind development.

1.2 Predicting how kittiwake populations will respond to novel impacts and changes in management measures

The third knowledge gap (KG3) relates to kittiwake population dynamics. Legislation requires assessment of the potential environmental impact of an offshore wind farm (OWF) development prior to consent. One major consideration in many recent consenting decisions in the UK has been the potential impact of additional mortality caused by OWFs on populations of kittiwakes. Unfortunately, in order to fully assess how a population is likely to respond to additional mortality from an OWF development, we need to understand the various drivers that determine kittiwake population size and status. For example, a population may decline after construction of an OWF nearby but there are many reasons why the observed decline might have occurred. If a population has capacity to demonstrate a compensatory density-dependent increase in one or other of its demographic rates, e.g. productivity, following a reduction in population size due to OWF mortality, the ultimate impact of the wind farm on a population will be less than in the absence of a density-dependent response.

This feasibility review aims to identify a set of potential research projects that could be undertaken in the near future to better understand likely consequences of OW development on kittiwake populations. The present review is informed by discussions with ecological consultants, OWSMRF Key Stakeholders and experts in seabirds, particularly kittiwakes, sandeels and other forage fish, population modelling and other relevant areas of work. On 25 February 2020, JNCC organised a workshop that aimed to identify research that would improve understanding of kittiwake population dynamics and drivers of population change in the context of offshore wind development. This workshop, held in Glasgow, was attended by experts in kittiwakes, their prey and population dynamics: James Chapman (University of Aberdeen), Signe Christensen-Dalsgaard (NINA), Aonghais Cook (BTO), Bob Furness (MacArthur Green), Cat Horswill (University of Glasgow), Jason Matthiopoulos (University of Glasgow), Julie Miller (University of Glasgow), Agnes Olin (University of Strathclyde), Mark Trinder (MacArthur Green) and Peter Wright (Marine Scotland Science), along with OWSMRF Key Stakeholders: Tom Evans (MSS), Mel Kershaw (NE), Matty Murphy (NRW) and Lucy Wright (RSPB), and OWSMRF Developers: Sophie Banham (Equinor), Paul Catterall (Innogy), Darren Jameson (SPR), Gareth Johnson (Ørsted), Jesper Kyed Larsen (Vattenfall), Nancy Mclean (EDF Renewables) and Christie Patterson (SPR), and JNCC staff running the workshop: Helen Baker, Sue O'Brien, Lise Ruffino, Danni Thompson. Some experts were unable to attend the meeting but subsequently provided input: Francis Daunt (CEH), Ian Mitchell (JNCC) and Kate Searle (CEH).

The high-level objectives of the workshop were:

A. Reduce uncertainty around current PVA (population viability analysis) modelling approaches through obtaining better evidence with which to parameterise PVA models;

B. Improve understanding of the wider context in which current typically colony-specific PVA approaches sit, e.g. the wider spatial scale at which population processes, such as meta-population dynamics and density dependence might be operating;

C. Identify drivers of change in kittiwake populations and their mechanism of operation to understand the relative impact of offshore wind development alongside other pressures, and options for managing pressures to inform discussions around IROPI/derogation-related management measures.

During the workshop, a review of current understanding of kittiwake population dynamics and drivers of population change was presented and critical gaps in our understanding were identified. Experts were then invited to suggest research that would help fill the gaps in the evidence base. Discussions covered the following topics: i. intrinsic drivers including metapopulation dynamics and density dependence; ii. extrinsic drivers that affect resource availability, including prey abundance and availability, e.g. climate change, commercial fisheries; iii. extrinsic drivers that directly affect demographic rates and interactions between intrinsic and extrinsic processes. At the end of the workshop, a selection of these ideas were discussed further in order to provide additional detail regarding what a research project might involve, risks and limitations, *etc*. JNCC then used the outputs of the workshop, in combination with further discussion with experts, as required, to fully understand each research opportunity, to inform this report. This JNCC feasibility review report describes in detail research opportunities that are likely to be of most benefit to OW development and reducing consenting risk.

2 Existing evidence and understanding

As stated above, this report looks at kittiwake population dynamics in the context of offshore wind development. Understanding the population dynamics and the wider drivers of population change of a species like kittiwakes, which is long-lived, highly mobile and is exposed to a variety of pressures both on land and at sea, requires a holistic approach.

The flow chart below (Figure 1) helps visualise the complex parameters, mechanisms and processes we need to understand in order to improve our ability to predict how kittiwake populations will respond to novel impacts, such as mortality at offshore wind farms. Ultimately, evaluating the magnitude of wind farm impacts on kittiwake populations requires accurate estimates of population size, as well as a good understanding of how kittiwake populations respond to variations in their demographic parameters. Population size is determined by demographic rates (e.g. adult survival, juvenile and immature survival, productivity, age at recruitment, immigration, emigration). These demographic rates can be altered by density-dependent processes, which can for example help compensate for increased mortality rates or exacerbate the rate of decline of a population. Demographic rates can also be affected by extrinsic factors. Some extrinsic factors, such as fisheries and climate change, will indirectly affect population size through changes in food availability and hence carrying capacity, whereas other pressures such as extreme weather conditions or predation at the colonies will have a direct influence on demographic rates.

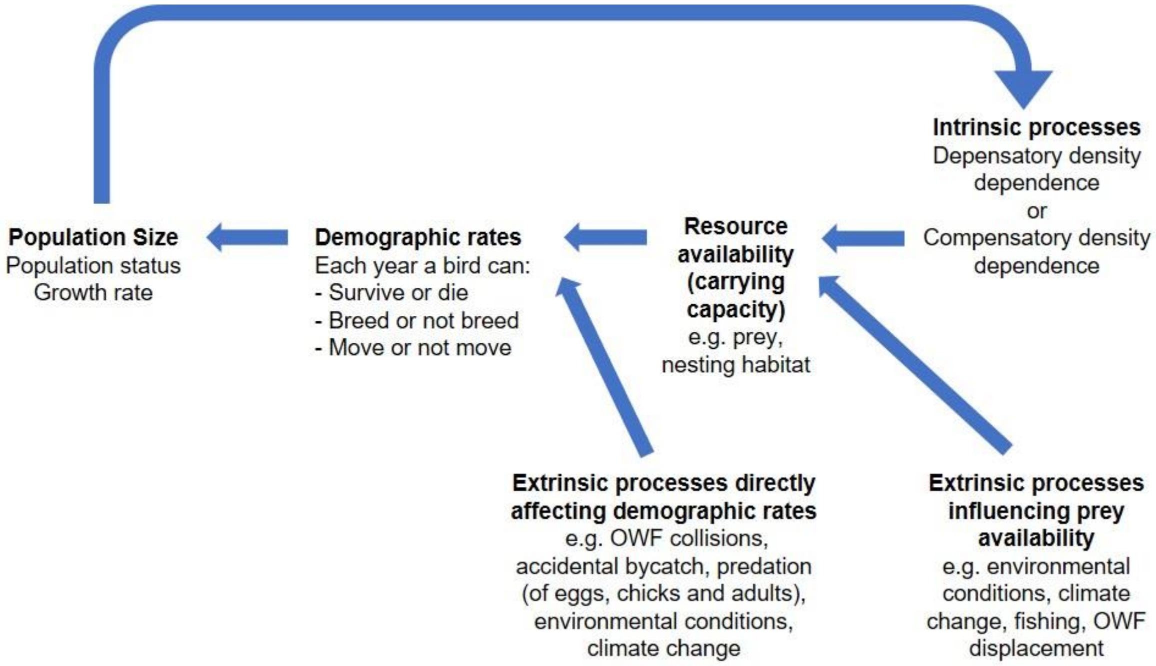

Figure 1. A flowchart to illustrate how extrinsic and intrinsic processes determine demographic rates and population size.

This section summarises the existing evidence base on both intrinsic and extrinsic processes regulating kittiwake populations. In particular, we provide evidence for the scale at which meta-population and density-dependent processes may operate in kittiwake populations, as well as the relative importance of environmental and anthropogenic factors driving kittiwake population dynamics, such as prey availability, fisheries, climate change and other pressures.

2.1 Kittiwake meta-population dynamics

Kittiwake colonies experience exchanges of individuals with other colonies. Among seabirds, kittiwakes have intermediate levels of dispersal, between very highly philopatric and site faithful species such as auks, and more mobile species such as terns. Long-term monitoring of kittiwakes at North Shields and Coquet Island, in north east England, revealed that natal philopatry was ≤50% (i.e. every year the number of recruits from other colonies exceeded the number of philopatric recruits) and those that returned to their natal colonies to breed were mostly males, perhaps to reduce inbreeding (Coulson & De Mevergnies 1992; Coulson & Coulson 2008). Ring recoveries (i.e. from dead birds) also indicated that, among the juveniles that dispersed from a UK colony, most of the recoveries in the year following ringing occurred within 600km (62%), up to 1500km (11%) and beyond (27%), of their natal colony, while older birds (>4 years old) ringed as chicks tended to be recovered closer (≤100km) to their natal colony (see Table 4 in Coulson & De Mevergnies 1992). Additionally, this study provided slight evidence for UK kittiwake meta-population dynamics following a bimodal pulse of relatively local recruitment within 50km and recruitment over much larger distances (400-900km).

GPS tracking of adult breeding kittiwakes in Hornøya, north-eastern Norway, indicate that prospecting movements could occur as early as within a week of egg failure (Ponchon *et al*. 2015) and at distances ranging from 1km to 40-50km away from their nesting sites (Ponchon *et al*. 2017, 2015). Comparative analyses of host (kittiwake) - parasite (ticks) structure in the North Atlantic revealed that kittiwake populations function at regional scales during the breeding season, with prospecting behaviour constrained to distances of 200km (McCoy *et al*. 2005).

For an adult kittiwake, the decision to leave a current breeding site and where to settle in subsequent breeding seasons was found to be dictated by its own breeding performance in the current year as well as perceived habitat quality such as breeding performance of conspecifics. In Hornøya, prospecting movements to new neighbouring colonies were only observed in failed breeders (Ponchon *et al*. 2015), although sample size was small in this study (12 experimentally failed breeders and 21 successful breeders studied). These findings were further supported by a long-term study of kittiwake sub-colonies in Brittany (Danchin & Cam 2002), which showed that birds that skipped one or several breeding seasons were 4.4 times more likely to disperse than birds that bred in successive years. However, prospecting movements do not necessarily lead to dispersal, as they entail additional costs (Danchin & Cam 2002). At the scale of a few neighbouring (sub-)colonies in Brittany, when breeders changed breeding cliffs following reproductive failure, they tended to select cliffs of per capita higher reproductive success (Danchin *et al*. 1998). In another study in Hornøya, Boulinier *et al.* (2008) manipulated the breeding success of a sample of kittiwake nests and found that failed breeders were 1.5 times more likely to leave their colony, and not return the following year, if the local level of breeding success of their conspecifics was low. Furthermore, the high return rate of GPS-tracked prospecting failed breeders (86%) observed in Hornøya – one of the most productive colonies in Eastern Finnmark – indicates that information from conspecifics may be more important than own breeding performance in selecting a breeding site (Ponchon *et al*. 2015). These studies therefore suggest that simplifying dispersal as a fixed movement rate, rather than a more dynamic, informed process, can be misleading, especially in rapidly changing environments (Ponchon *et al*. 2014). The development of technology allowing tracking movements of both successful and failed breeders over multiple seasons with high levels of spatial and temporal accuracy should provide some insight on the spatial scale and directional patterns of post-breeding movements, as well as the processes underpinning between-colony connectivity in contrasting environments (Boulinier *et al.* 2008)

Meta-population theory predicts that in order to maintain total population size in the long-term, while buffering spatial and temporal environmental change, individual birds need to be able to escape poor local quality patches while retaining breeders on higher quality patches. Ponchon *et al*. (2014) modelled kittiwake population size and persistence under varying dispersal strategies and environmental conditions. They found that informed dispersal decisions (i.e. both the decision to leave and where to settle is informed by personal and social cues) created extinction-colonisation dynamics and could play a major role in helping species keeping pace with environmental change (i.e. birds track changes in breeding habitat quality by selecting better patches, either currently used, previously used or never used). These dynamics promoted asymmetrical distribution of breeding colonies, with a larger number of successful breeders in better quality colonies and a high extinction probability of the poorest colonies. On the other hand, random (i.e. not informed) and semi-informed (i.e. decision to leave the colony is informed by personal and social cues but choice of where to settle is random) decisions created source-sink dynamics, where the constant emigration of individuals to both “good” and “bad” colonies prevented local extinction, while the low carrying capacity of “bad” colonies prevented increases in colony size through rescue effects. A fourth scenario whereby individuals were not allowed to move between colonies (strict philopatry) led to high extinction probabilities in all colonies, which was exacerbated in highly spatially and temporally variable environments.

The fact that some regional kittiwake populations in the North-East Atlantic are in decline indicate that some of them are not coping well with ongoing rapid changes in environmental conditions, in addition to other natural and anthropogenic pressures (e.g. Sandvik *et al*. 2014). Although there is good evidence of connectivity between clusters of colonies in the North-East Atlantic (e.g. Frederiksen *et al*. 2005a), in most parts of the species’ breeding distribution range, the true spatial population dynamics of connectivity between colonies – i.e. movement distances, directions and rates – remains unknown. Determining what role (“bad” or “good”, “source” or “sink”) each colony or region may play within a meta-population, and how this role may vary over time, is crucial to ensuring conservation efforts are directed to where they are most needed. It is perhaps more likely that these source-sink dynamics operate at a larger scale than individual colonies, since demographic rates can be affected by regional variation in food availability (Olin *et al*., in press).

Accounting for connectivity among kittiwake colonies is key to assessing population vulnerability. It is important to note however that movement data (tracking, capture-mark-recapture) alone are not sufficient to address source-sink questions. Demographic data (survival and productivity) should ideally be combined with movement data to better understand meta-population processes. Abundance and demographic data that provide information on population change is a priority. Thanks to the several long-term monitoring studies on kittiwake colonies in Britain, Ireland and Norway, we have now gathered substantial information on productivity; however, our knowledge of kittiwake survival, especially across juvenile and immature age classes, remains poor.

2.2 Density dependence in kittiwake populations

Density dependence is recognised as a driving force regulating animal populations in the wild. Under compensatory (or negative) density dependence, carrying capacity limits population growth. Depensatory (or positive) density dependence, on the other hand, accelerates population decline when numbers become depleted under a critical threshold. Therefore, ignoring density dependence can lead to misleading population projections. Compensatory density dependence is particularly important in central place foragers. Furness and Birkhead (1984) showed that the size of a kittiwake colony is strongly influenced by the number of kittiwakes breeding in other nearby colonies, providing strong evidence for density dependence limiting breeding numbers. The interpretation by Furness and Birkhead (1984) was further supported by more recent work (Wakefield *et al*. 2013), which interpreted these spatial patterns as caused by density-dependent competition between colonies leading to spatial segregation of the utilisation distributions of adjacent colonies (see also Wakefield *et al*. 2017). Moreover, studies in Norway found a strong relationship between colony size of kittiwakes (and other common seabirds) and local abundance of forage fish (Sandvik *et al*. 2016). Those authors concluded that large colonies were located where travel distances to foraging hot spots were minimised, which further supports the interpretation that breeding seabirds tend to be strongly influenced by food supply around their colonies, with a density-dependent limit to breeding numbers set by breeding season food supply.

Furthermore, Coulson (2011) showed that the annual rate of increase in size of 46 kittiwake colonies in the UK between 1959 and 1969 was inversely related to colony size. Colonies of 1-10 pairs in 1959 increased on average by 70% up to 1969. Colonies of 10-100 pairs in 1959 increased on average by 20% up to 1969. Colonies of 100-1000 pairs in 1959 increased on average by 5%. Colonies of 1000-10,000 pairs in 1959 increased on average by 3%. This implies strong compensatory density dependence. It is unclear just from these changes in numbers which particular demographic parameters were affected, but Coulson (2011) inferred from his detailed observational studies, and from population modelling, that the main reason for the progressive differences in growth of an individual colony was the balance between immigration and emigration of immature birds.

A compensatory density-dependent reduction in colony growth rate is also clearly evident from data on colony size over a period of decades for individual colonies that have been studied in detail. Numbers at Marsden (Tyne & Wear) showed a rate of increase that progressively slowed as numbers grew (Coulson 2011, Figure 11.5). Numbers at nearby Coquet Island (Coulson 2011, Figure 11.6) showed similar trend with colony size. However, numbers grew rapidly at Coquet Island when growth had virtually ceased at Marsden (in the 1990s). This shows clearly that the rate of growth was a colony-specific feature related to local competition and was not a consequence of region-wide variations in conditions.

Long-term monitoring of breeding kittiwakes at North Shields (e.g. Coulson 2011; Porter & Coulson 1987) has shed some light on the possible mechanisms by which density dependence may operate. In response to an increase in adult mortality rate in the mid-1980s, field data indicated that kittiwakes started breeding at an earlier age, the number of recruits increased and the proportion of non-breeding adults in the population declined. A change in age at first breeding of over 1 year (from 4.59 years in 1961-70 to 3.69 years in 1981-90) can have a strong density-dependent influence on the rate of population growth in a long-lived species.

Measuring the strength and describing the shape of density dependence typically requires long-term time series of population count or demographic data. By reconstructing the population size of Black-legged kittiwakes in Alaska from historical records, Goyert *et al*. (2017) revealed significant changes in carrying capacity (i.e. breeding numbers) over a 40-year period, which suggests that kittiwakes may be able to cope with unpredictable environments, to some extent. The authors also found evidence for negative density dependence on population rate of change, with no time lag: population size fluctuated around estimated carrying capacity so that drops below the threshold were followed by recovery, and vice-versa. On the other hand, modelling the effects of the Exxon Valdez oil spill in 1989 revealed a sharp decline in carrying capacity and a subsequent drop in kittiwake population size for three consecutive years, followed by a slight increase to a stable level below carrying capacity for further six years, possibly revealing effects of delayed recruitment. It is worth noting however that the way missing data were imputed to reconstruct annual count data in this study (by calculating averages) has less power than an integrated framework where information from population dynamic processes is used to fill in gaps in count data (e.g. Miller *et al.* 2019).

In another modelling study using Bayesian state-space population models to reconstruct historic kittiwake breeding numbers from the Isle of May, Miller *et al*. (2019) evaluated population persistence under contrasted scenarios of extrinsic (i.e. environmental) and intrinsic (i.e. density-dependent) population regulation, assuming either closed or open populations. Compensatory density dependence acting on productivity (i.e. where a penalty is applied to intrinsic productivity as population size increases) was applied in the model. Model outputs showed that kittiwake populations that were open to immigration were predicted to increase under low levels of environmental stochasticity, but then declined to eventual extinction above a higher threshold of extrinsic regulation (i.e. populations may only be able to compensate for the negative impacts of external pressures up to a certain level of impact). This modelling exercise allowed predicting a defined parameter range for the strength of density-dependent regulation in Isle of May kittiwakes (see Supporting Information in Miller *et al*. 2019).

In a meta-analysis of time series of seabird population counts, Horswill *et al*. (2017) found that, while the strength of negative density dependence appeared consistent between species and colonies (n=1 colony for kittiwakes), the mechanism by which productivity was regulated was highly context-dependent with a similar number of studies reporting compensatory, depensatory and no apparent effects. Their literature review highlighted that, for kittiwakes, compensatory processes were the most frequently reported density-dependence mechanism.

It also worth noting that no density-dependent relationship between kittiwake breeding success, and/or growth rate, and colony size was found in three regional-scale studies (Britain and Ireland, Frederiksen *et al*. 2005b and Carroll *et al*. 2015; Norway, Sandvick *et al*. 2014). It is likely that the strength of density dependence in kittiwake populations depends on spatial and temporal variations in prey availability. For example, Trevail *et al.* (2019) found that in areas with greater resource patchiness, kittiwakes undertook longer foraging trips, spent proportionally more time foraging while away from the colony, overlapped more with other individuals and had reduced breeding success. These results suggest that there is greater competition between individuals for finite resources in more heterogeneous environments, which comes at a cost to reproduction. At spatially homogenous levels of prey availability, dispersal distances and rates will dictate the regional scale of the density dependence effect, so that the global kittiwake population will be divided into smaller local populations with effectively independent dynamics. Conversely, when prey distribution is spatially and temporally structured, a negative relationship between colony size and productivity would not necessarily be expected across regional scales since carrying capacity is not the same everywhere (typical case of the kittiwake-sandeel system in the North Sea; Frederiksen *et al*. 2005b; Olin *et al*., in press). In addition, rates of annual population change, rather than colony size, may be more informative to infer food-driven density-dependent processes over large spatial scales.

Compelling evidence from field observations and modelling of population dynamics supports the fact that compensatory density-dependent processes play an important role in regulating kittiwake populations. However, the underlying empirical evidence is patchy, especially at the level of both specific colonies and regional populations of conservation interest. Crucially, there is a lack of understanding of the wider range of density-dependent mechanisms, the spatial scale at which they may operate, and the factors driving the strength and shape of the density-dependent relationship. It is worth noting though that obtaining robust evidence of density dependence is difficult as a result of sampling errors, short time series and confounding effects with rapidly changing environmental conditions. In addition, populations of long-lived species can respond to changes in carrying capacity with a time lag of several years, which renders the detection and characterisation of these processes challenging.

Evidence for positive density-dependent regulation of kittiwake populations is scant and this contrasts with other seabird species (Horswill *et al*. 2017). However, this could simply reflect survey effort and the challenges of modelling depensation, especially as many of colonies studied in the UK may not be small enough to permit empirical extrapolation, although some colonies in southern England have seen declines and colony abandonment (pers. comm. M. Kershaw, Natural England). Determining the critical density threshold under which depensation exacerbates kittiwake population decline would be valuable. Detecting depensatory demographic processes in long-time series of count data can be challenging due the confounding effect of environmental stochasticity and social effects, in addition to the effect of, for example, predation. Social effects are strong in kittiwakes; birds breeding at the centre of a colony tend to have higher survival or productivity; yet this is not a manifestation of positive density dependence. Field observations indicate that predation of nests and chicks can drive kittiwakes to leave a colony (e.g. Norway, Shetland, North Shields). While there are few kittiwake colonies where predation appears to be a major issue, the extent to which it can contribute to the decline of depleted colonies or populations is largely unknown.

2.3 Impact of prey abundance, availability and quality on kittiwake demographic rates

Kittiwakes are obligate sea surface feeders – i.e. they are able to capture prey only within the top metre of the sea surface. Throughout most of their range, kittiwakes prey almost entirely on small fish (<100mm long) during the breeding season. In the North-East Atlantic, the lesser sandeel (*Ammodytes marinus*) makes up a major component of kittiwake diet during the breeding season, although other fish species, such as sprat (*Sprattus sprattus*), capelin (*Mallotus villosus*) and young herring (*Clupea harengus*), replace them in areas where sandeels are uncommon (e.g. Bull *et al*. 2004; Lauria *et al*. 2012). Sandeels are available to sea surface predators only during a relatively short period of time. They have a dependence on sandy substrate, where they overwinter (which can extend from August to April). In the North Sea, they emerge from the sand to spawn their demersal eggs between December and February. Their larvae hatch between February and April and the planktonic larvae are transported by currents for 7-10 weeks. Older sandeels are active in the water column until early summer, emerging only during daylight hours in order to feed.

Breeding adult kittiwakes eat sandeels aged one year or older (hereafter 1+ group) during April and May and then switch to young of the year (hereafter 0-group) sandeels for both themselves and their young in June and July, as juvenile sandeels become available (Harris & Wanless 1997; Lewis *et al*. 2001). On the Isle of May and across the Shetland isles, kittiwake breeding success was found to be related to sandeel abundance and availability of both 0- and 1+ groups (e.g. Daunt *et al*. 2008; Poloczanska *et al*. 2004; Rindorf *et al*. 2000). At regional scales, kittiwake breeding success synchronises with spatial aggregations of sandeels, forming three geographically distinct main clusters in British waters (Frederiksen *et al*. 2005b; Olin *et al*., in press). On Foula, Shetland, low availability of 0-group sandeels negatively affected adult kittiwake survival (Oro & Furness 2002), which indicates that young-of-the-year sandeels may play an important role for adult kittiwakes in replenishing body reserves following breeding while older sandeels tend to remain buried in the sand in early summer and have thus become unavailable to kittiwakes.

There is no clear evidence that sandeel availability at the sea surface is distinct from sandeel abundance in the water column (obtained through stock assessments). This relationship is however subject to a strong seasonal effect. This means that a positive relationship between both metrics can be observed only if abundance data are collected during the period when breeding kittiwakes are feeding on them (i.e. from end March to July/August in the UK). Timing of availability is extremely important in this context: kittiwakes may not have access to sandeel prey (especially young of the year) if sandeel eggs hatch too early in the season due to an early spring bloom and early appearance of copepod prey for example (see section 2.1.5 for further details). The abundance-availability relationship can also be affected by spatial effects if abundance data is not collected in areas known to be used by foraging kittiwakes during the breeding season. More generally, availability of sandeel prey to breeding kittiwakes should be assessed when sandeels are active in the water column and within foraging areas of kittiwakes.

Long-term diet studies on the Isle of May have highlighted a long-term decline in the overall prevalence of sandeels in kittiwake chick diet, concomitant with an increase in the relative prevalence of clupeids in Scottish waters (Wanless *et al*. 2018). Several studies indicate that kittiwakes are able to switch forage fish prey, and this may help sustain their populations in areas where sandeel removal by commercial fisheries is substantial. There is also evidence of temporal changes in sandeel quality, with a long-term decline in mean annual lengths of 0-group and 1+ groups fed to chicks despite constant energetic value per gram of fish (e.g. Burthe *et al*. 2012; Wanless *et al*. 2018). However, the decline in the overall energetic value of the fish fed to chicks did not have discernible detrimental effects on kittiwake breeding success on the Isle of May (Burthe *et al*. 2012). On Anda Island, Norway, a higher mesopelagic fish/sandeel ratio fed to chicks translated into a decrease in chick survival (Christensen-Dalsgaard *et al*. 2018), but this was related to longer, and hence more costly, trip distances and durations to catch their prey.

There is little information on what kittiwakes feed on outside the breeding season. Some studies have indicated that kittiwakes are able to switch from fish to invertebrate prey during the winter months (see Coulson 2011). Equipping adult kittiwakes with light-based tracking devices (GLS) has allowed the identification of important over-wintering areas of kittiwakes breeding in the North and Norwegian Seas (see SEATRACK portal). This information can then be used to link environmental conditions and prey abundance in areas known to be used by adult kittiwakes in the autumn and winter months with their demographic parameters. For example, in Hornøya, variation in annual adult survival rates was related to temporal variation in capelin density in kittiwakes' non breeding areas identified by GLS tracking (Reiertsen *et al*. 2014). However, correlative studies cannot reveal exact mechanisms – e.g. it may not be plausible that kittiwakes feed on capelins in non-breeding areas as seas there are far too deep (P. Wright, pers. comm.). Inferring effects on immature birds using information on the non-breeding distribution of adults should also be treated with caution (see e.g. Sandvick *et al*. 2014).

2.4 Impact of industrial fisheries on kittiwake demographic rates

The largest single-species fishery in the Greater North Sea harvests the lesser sandeel. Total annual landings fluctuated over the past 70 years, with up to a million tonnes in the late 1990s down to below 500 000 tonnes in the last 15 years (ICES 2019). Sandeel fisheries occur in April–June and mainly target one year or older sandeels (1+ group). Some of the areas targeted by fisheries are also used by foraging kittiwakes during the breeding season and there is good evidence that some kittiwake populations in the North Sea are negatively affected by sandeel removal by commercial fisheries. Frederiksen *et al*. (2004) modelled the effect of the presence of the Wee Bankie sandeel fishery (40km off the east coast of Scotland) on kittiwake demographic rates on the Isle of May between 1986 and 2002 and found a reduction in adult survival when the fishery was active. The study also showed that the average breeding success was significantly lower when the fishery was active (0.30 fledged chicks/nest [95% CI 0.26-0.34]) than before it was active (1.07 fledged chicks/nest

[95% CI 1.00–1.14]). This pattern was confirmed at regional scales, with a larger number of sampled kittiwake colonies along the east coast of Scotland (Frederiksen *et al*. 2008): the average breeding success was significantly higher (0.72 chicks produced/nest) in the Wee Bankie fishery closure area compared to neighbouring areas where the fishery was active (0.32 chicks produced/nest). Correlative analyses between sandeel fishing mortality in the Dogger Bank region (~100km from the UK coast) and kittiwake productivity at Flamborough and Filey Coast SPA revealed a similar negative relationship, but with a two year lag effect, suggesting a more complex link (Carroll *et al*. 2017). Furthermore, kittiwake breeding success was negatively linked to fishery effort indices - denoted as a product of vessel size and the number of days spent in the area in Frederiksen *et al.* (2008) - and by the interaction between the sandeel population size and the proportion of the population harvested (Cook *et al*. 2014).

The mechanisms by which sandeel fisheries affect kittiwake demographic rates are not always clear and can be diverse. As fisheries target sandeel age classes comprising one- and two-year olds, they can directly compete with kittiwakes at a local level in the months of March to July. The timing of the fishery relative to the timing of the switch in kittiwake diet from 1+ group to 0-group sandeels can be crucial in determining impacts on both kittiwake breeding success and adult overwinter survival in the current year. Effects in subsequent years are also likely to accrue through the overall reduction in the abundance of older sandeels. If fishing reduces the spawning stock to the point where egg production limits the numbers of 0-group fish, recruitment of 0-group sandeels may be reduced in subsequent years, explaining therefore the two year lag effect observed in Flamborough and Filey Coast SPA (Carroll *et al*. 2017). The question of the absolute impact of commercial fisheries on sandeel populations should not be addressed only by evaluating how much stock biomass is reduced at a given point in time, but also via looking at temporal variation in biomass.

Recruitment is one key variable to look at: sandeels usually become mature at age 2 years and trends in biomass appear to correlate with trends in recruitment with a two-year lag (Wright 1996). The prediction is then that heavily fished stocks are more dependent on sandeel recruitment from the previous year to sustain their populations (as fewer sandeels survive past age 1 year). Conversely, fishery closure can increase resilience in sandeel populations by reducing age truncation and the dependence of local spawning on first time spawners. As a consequence, in fishery closure areas, there may be less variability in sandeel annual biomass, which can benefit their predators. Nevertheless, the relative benefits of fishery closure on sandeel stock is likely to vary among regions, as observed in Shetland and off the Scottish east coast where variations in environmental conditions are the main drivers of low sandeel recruitment (Poloczanska *et al*. 2004; Régnier *et al*. 2019; van Deurs *et al*. 2009).

Environmental and fishery effects can interact in a complex manner, so that individual effects can be difficult to tease apart. Some studies found support for additive effects of climate change (through increases in sea surface temperature and advancement of timing of the spring bloom) and the presence of active sandeel fisheries on kittiwake breeding success (Frederiksen *et al*. 2004; Scott *et al*. 2006) and adult survival (Frederiksen *et al*. 2004). Moreover, Scott *et al*. (2006) found that the observed effect of the advancement of the timing of the spring bloom did not differ between years when fishing was active or non-active. It is possible, however, that in some circumstances both effects interact, such that when environmental conditions are poor, fisheries could exacerbate a difficult situation for seabirds by further reducing the biomass of available 1+ group fish (Rindorf *et al*. 2000).

2.5 Impact of climate warming on marine trophic webs, including kittiwake populations

Global warming of our seas is predicted to have knock-on effects on marine predators. The Black-legged kittiwake is one of the most intensively monitored seabird species in UK waters. As kittiwakes are surface feeders specialising on one or very few species of forage fish, they are likely to be affected by changes in physical and biological oceanic conditions occurring throughout the water column and at lower trophic levels, making them a useful indicator of the state of marine ecosystems.

Long-term kittiwake population monitoring in some British, Irish and northern Europe colonies have provided the opportunity to relate demographic responses to indicators of climate change, e.g. rising Sea Surface Temperature (SST). In the North Sea, previous studies have provided support for a negative relationship between kittiwake breeding success and SST in February and March of the previous year (Cook *et al*. 2014; Frederiksen *et al*. 2004), and for a negative relationship between kittiwake adult survival and SST of the current year (Frederiksen *et al*. 2004). Further work reported negative correlations between winter SST and kittiwake productivity across multiple colonies in the UK (Frederiksen *et al*. 2007), and indicated that kittiwake breeding success in Britain and Ireland synchronised in relation to spatial aggregations of sandeels (Frederiksen *et al*. 2005b). These findings led the authors to suggest that SST was driving kittiwake breeding variability through effects on their main forage prey, possibly through reduced sandeel recruitment in warmer winters leading to lower availability and or abundance of 1-year old sandeels early in the breeding season the following year.

The bottom-up effect of lagged spring SST on kittiwake productivity has been shown to vary in strength among colonies and regions. For example, several studies have found only weak support for an indirect link between SST and kittiwake productivity both in eastern Scotland (Eerkes-Medrano *et al*. 2017) and across Britain and Ireland *(*Carroll *et al. 2015;* Cook *et al*. 2014; Lauria *et al*. 2013, 2012). Furthermore, at Fowlsheugh SPA, kittiwake breeding success was related to 0-group sandeel abundance only when two of the twelve years of data were removed from the analysis, indicating other factors were also important (Eerkes-Medrano *et al*. 2017). These mixed results probably reflect the complex physical and trophic relationships that determine the structure and functioning of oceans; some of the processes may operate differently across spatial scales and among marine regions (e.g. the importance of sandeels to breeding kittiwakes can differ between regions).

The ‘SST-kittiwake productivity’ relationship was explored further by adding copepods (*Calanus spp.*), an important prey for sandeels, into the equation. However, no clear consistent pattern seemed to emerge across studies and scales. While a positive link was found between copepod biomass in Eastern Scotland, the abundance of sandeel larvae and kittiwake breeding productivity on the Isle of May (Scott *et al.* 2006), this relationship did not hold in another colony in East Scotland (Fowlsheugh SPA), across North Sea regions (Frederiksen *et al.* 2007) or in the North-East Atlantic (Lauria *et al.* 2013). Moreover, no consistent patterns emerged from looking at the relationship between kittiwake productivity and previous year’s abundance of copepods within North Atlantic regions (Frederiksen *et al.* 2013, 2007).

The apparent absence of consistency in the relationship between physical factors and fish and/or kittiwake demographic parameters among studies indicates that the use of simple environmental proxies can be misleading, as these correlative relationships are likely to miss important mechanistic processes affecting sandeels (Eerkes-Medrano *et al.* 2017). The impact of climate change on sandeels is complex; it can affect sandeels both directly, via increases in their metabolic rate, and indirectly through variation in the production cycles of their zooplankton prey. Furthermore, rising SST differentially affects sandeel gonad development (Wright *et al.* 2017b, 2017a), egg development (Régnier *et al.* 2018) and copepod development rates (Cook *et al.* 2007), so that no simple cause-effect relationship between temperature and fish exists. Crucially, a major determinant of the number of larvae hatched in a given year is the phenological synchrony between sandeel and their larval prey (Régnier *et al.* 2017), which can be disturbed by rising sea surface temperatures. While warming temperatures delays sandeel spawning times through a delay in ovarian development, it also advances the seasonal peak of plankton blooms and hence the emergence of copepod prey (Régnier *et al.* 2019). A trophic mismatch between sandeel hatching time and availability of their copepod prey has been documented on the southeast coast of Scotland in recent years, in relation to the rate of sea temperature decline between September and February and average February temperatures (Régnier *et al.* 2019b). Modelled climate warming scenarios further predicted a phenological mismatch between copepod egg production and sandeel spawning reaching up to 41 days by 2050, resulting in a predicted decline in sandeel recruitment (Régnier *et al.* 2019).

A delay in sandeel spawning and hatching times can also create a temporal mismatch between the availability of forage fish later in the year and peak energy demand periods for breeding kittiwakes, so that a late appearance of young of the year sandeels at the sea surface can lead to low chick survival in kittiwakes (Lewis *et al.* 2001). On the Isle of May, kittiwakes have delayed breeding from 1983 to 2006 to track the timing of 0-group sandeels attaining a threshold size, yet these shifts were not sufficient to keep pace with changes in sandeel length (Burthe *et al.* 2012). However, this apparent decline in prey quality did not translate into a decrease in breeding success. Other pressures, and/or the abundance or timing of availability of alternative prey, could represent more important drivers of variation in kittiwake breeding success on the Isle of May.

Climate-driven changes in oceanographic processes that determine the availability of forage fish at the sea surface during energy-demanding times of year also need to be considered. For example, seasonal stratification timing and strength, as well as timing of the spring bloom, influence the timing of emergence and movements of both zooplankton and their sandeel predators through the water column, which ultimately determine feeding conditions for kittiwakes at the sea surface (Carroll *et al.* 2015; Scott *et al.* 2006). The fact that kittiwakes avoid foraging in very strongly stratified areas (Scott *et al.* 2010) and that they breed less successfully in years when the spring bloom and stratification occurred earlier (breeding success increased by 0.13 chicks/pair for every five days delay in timing of the spring bloom on the Isle of May; Scott *et al*. 2006) indicates that the impacts of climate change on kittiwake populations cannot be fully understood without learning from the physical environment.

While it is clear that some kittiwake populations have markedly declined over the past decades, and global warming of our seas may have contributed to a decrease in breeding productivity and/or adult survival, the exact mechanisms explaining these observed changes are likely to be varied and complex. The strength of marine trophic relationships is expected to vary both in space, due to differing physical and biological mechanisms operating at the scale of a colony vs. regional population, and in time due to the predicted species distribution range shifts as SST increases (e.g. Frederiksen *et al.* 2013). Furthermore, changes in oceanographic conditions can affect seabirds at both their breeding and non-breeding foraging areas, with potential lag effects of a decline in immature survival during the autumn and winter months on population growth rates (e.g. Sandvik *et al.* 2014).

2.6 Other pressures affecting kittiwake demographic rates

In addition to changes in prey abundance, availability and quality, kittiwakes face other pressures both at the colonies and at sea. Both adult and young kittiwakes experience predation at the nests from a variety of predators, e.g. large gulls, skuas, corvids and raptors. Predation rates may be exacerbated when predators' main prey abundance is reduced, as found in Newfoundland as a consequence of changes in sea temperatures and delayed capelin availability to large gulls (43% and 30% of kittiwake eggs and chicks, respectively, were taken by herring gulls and greater black gulls on Gull Island; Massaro *et al.* 2000) and in Shetland where the concomitant increase in great skua numbers and decrease in sandeel availability correlated with an increase in adult kittiwake and chick mortality rates (Heubeck 2002; Oro & Furness 2002). Despite larger colonies being more conspicuous and attracting more predators, predation rate by large gulls was found to decrease as the size of kittiwake colonies increased in Canada, due to a dilution of predation risk in large colonies (Massaro *et al.* 2001).

Weather conditions can affect kittiwake reproductive performance by reducing chick growth rates (e.g. reduced provisioning) and survival (e.g. due to nests being washed away) (Christensen-Dalsgaard *et al.* 2018). For example, extreme weather conditions such as the storm that hit the Isle of May in 2011 caused a net reduction in annual kittiwake population production of 10.7% (kittiwakes breeding in sections of cliffs exposed to the storm had a much higher rate of failure than those which were sheltered) (Newell *et al.* 2015). In their study on Anda Island, Norway, Christensen-Dalsgaard *et al*. (2018) found that under strong wind conditions, a higher sandeel/mesopelagic fish ratio in chick diet contributed to dampening weather effects on chick growth rate. This interaction could be important when considering impacts of climate change via changes in forage fish availability and abundance.

At sea, kittiwakes can suffer mortality from incidental by-catch in fisheries. Compared to the more documented impact of longline fisheries, the impact of gillnet fisheries on seabirds remains poorly known. A study in Norwegian waters reported 43% of surface-feeding seabirds in the by-catch, with kittiwakes making up 6.1% of the 52,000 seabirds by-caught over 10 years of survey (Bærum *et al.* 2019). Scaring lines and reduction in the release of wastewater during fishing operations are considered most effective mitigation measures in reducing bycatch rates of surface feeders.

While foraging at sea, kittiwakes may be exposed to contaminants, with potential sub-lethal effects on breeding performance. One study found a correlation between the probability of skipping reproduction in Svalbard kittiwakes and high levels of mercury – an endocrine disruptor – in blood (Tartu *et al.* 2013). In the same study site, lower apparent survival was linked to higher levels of certain persistent organic pollutants, but not mercury levels, in female kittiwakes (Goutte *et al.* 2015). Moreover, Svendsen *et al*. (2018) found higher levels of persistent organic pollutants in kittiwakes correlated with poorer body condition. These three studies do not prove causation, only correlation, and other potential confounding factors, such as age and bird quality could have influenced the patterns observed. (Svendsen *et al.* 2018)

Changes in fishery discarding may represent a new threat to kittiwake populations. Kittiwakes do exploit fishery waste extensively, especially in winter (Garthe *et al.* 1996). This food supply in UK waters has been greatly reduced over recent decades (Sherley *et al.* 2020).

Management of commercially fished species, leading to increases in numbers of predatory fish species, such as cod, can lead to increased predation on sandeels as these fish predators will be more efficient and capable of capturing sandeels than surface feeders such as kittiwakes. Consequently, fish predators can outcompete kittiwakes.

Other potential sources of kittiwake mortality and reduced productivity include diseases and parasites, weather conditions affecting water quality and visibility, competition with other seabirds and marine mammal predators for food, oil pollution, indirect effects of underwater noise (e.g. seismic activity) on sandeels, disturbance from tourism, and collision, displacement and barrier effects from offshore wind farms.

Better understanding of how these various pressures interact with each other and affect the long-term persistence of kittiwake populations in the context of predicted large-scale changes in carrying capacity is key.

3 Gaps in understanding

In order to assess with confidence, the impact that predicted mortality from offshore wind development will have on kittiwake populations, it is essential to understand what determines kittiwake population size. For example, what is currently maintaining population size at Flamborough and Filey Coast SPA? Is it survival of adults and recruitment of young birds from that colony or is it immigration from another colony, or both? Population response to additional wind farm mortality on adults breeding at Flamborough and Filey Coast SPA will vary depending on which processes are maintaining population persistence.

Considering individual seabird colonies as part of a larger ensemble of colonies or populations that exchange individuals and are regulated by density dependence allows for rescue effects (through immigration) and compensatory demographic effects (e.g. through an increase in productivity) in those colonies and populations that are in decline. In the absence of empirical evaluation of connectivity, as well as the shape and strength of density dependence, a common approach in impact assessments is to use closed population models with no density dependence. Yet populations affected by offshore wind development would be predicted to respond very differently to additional mortality if these processes were included in population models.

Each kittiwake colony size could be regulated in a slightly different way, for example, by acting as a source or a sink population. Furthermore, this is likely to vary with time as prey resource changes. Consequently, the particular demographic parameters and regulatory processes which are most important to quantify, in order to increase confidence in model predictions, will vary across colonies. It is therefore important to not look at individual colonies in isolation but as part of a meta-population, with regulatory processes acting on colonies over different temporal and spatial scales. Despite kittiwakes being one of the best-studied seabird species, we currently have a very poor understanding of metapopulation dynamics and the role of density-dependence in determining population size.

Understanding current pressures that kittiwake populations may already face, or will be facing in the near future, is essential for understanding the relative impact of offshore wind development on kittiwakes as well as how populations might respond to changes in management of those pressures. One of the most important pressures that kittiwakes are currently facing is a rapid change of food availability and quality, due to a combination of effects from fisheries and climate change. Whilst there is some evidence of the relationship between prey availability, sea surface temperature and kittiwake demographic rates, the mechanisms driving this relationship and likely change in demographic rates in response to new management of pressures is not known. In particular, there is considerable uncertainty in the spatial scale and rates at which changes in prey availability are likely to occur and how the demographics of breeding kittiwakes may respond to these changes.

Above all, understanding how population persistence is influenced by a combination of complex factors and regulatory processes, and ultimately what measures could be realistically considered in order to effectively compensate for additional mortality from wind farms, requires a holistic approach. Despite the often large amounts of uncertainty that surround demographic parameters and the regulatory processes that operate at certain kittiwake colonies, we can use the valuable knowledge acquired from long-term monitoring programmes, such as the Seabird Monitoring Programme, along with sophisticated modelling approaches, to understand how kittiwake populations are likely to respond to offshore wind farm mortality.

4 Potential research opportunities to improve understanding of kittiwake population dynamics

Below is a list of twelve Research Opportunities (RO) that experts suggested as potentially providing useful information for improving our understanding of kittiwake population dynamics, particularly how populations might respond to additional mortality from wind farms and which conservation measures are likely to be most effective. These research opportunities are a combination of both large-scale strategic approaches and smaller-scale mechanistic approaches, with varying timescales and resource requirements. All project ideas presented below are of direct relevance to reducing consenting risk in the context of rapidly increasing offshore wind development in UK waters.

Recently, Statutory Nature Conservation Bodies have advised that some offshore wind developments will have an adverse effect on site integrity for kittiwake features at certain SPAs, e.g. Flamborough and Filey Coast SPA and Forth Islands SPA. In order to better understand the way these populations are likely to respond to additional mortality and to identify the most effective measures to compensate for additional mortality, it is necessary to look at kittiwake population dynamics over a wider spatial scale (i.e. at the scale that ecological processes function). For example, to understand what maintains population size at an SPA, we need to know whether breeding adults are coming from another colony acting as a source for the focal SPA. Most of the Research Opportunities presented below therefore involve many kittiwake colonies, not only those of immediate current interest with respect to offshore wind development. However, when structuring work under these ROs, it will be important to bear in mind the objective of better understanding population dynamics at these focal colonies.

This section provides information on research opportunities that the authors, experts and Key Stakeholders thought were of the most direct benefit in order to (1) improve parameterisation of current PVA approaches, (2) provide wider context to current PVAs, and (3) provide evidence to inform discussions around conservation measures. Research Opportunities below are broadly grouped into two sections. The first section describes ROs (RO3.1-RO3.7) that will improve confidence in current PVA approaches, through improved parameterisation of current PVA approaches and/or through providing wider context and more biological realism. The second group of ROs describes research that would improve understanding of how current drivers of change, e.g. prey availability, influence kittiwake populations and how kittiwake populations might respond to changes in management of these drivers (RO3.8-RO3.12).

One key challenge in the assessment of predicted impacts from development of offshore wind is being able to predict how protected populations of seabirds will respond to additional mortality. Quantifying impacts of wind farms at the level of populations requires a robust understanding of the many factors, mechanisms and processes that often interact with each other to regulate these populations. The processes regulating kittiwake – and more generally seabird – populations can be complex and collecting empirical data on every population parameter for every colony is not feasible due to logistical and financial constraints.

However, the amount of data that is being collected annually at UK colonies, as well as the wealth of experts' knowledge, is substantial; the UK holds some of the world's best studied populations and some of the best expertise. Sophisticated and state-of-the-art modelling approaches can be developed to make use of the different types of knowledge available, while incorporating more biological realism, and hence reducing uncertainty around the population parameters of interest. These models are also flexible in how they work; they can integrate new data and types of information as they become available through, for example, future field studies. This is why a number of ROs presented in this report are based on modelling rather than field studies. These models are built on a similar structural base, which can be adapted to different types of datasets and extended to test various hypotheses and address different ROs, leading to synergies and efficiencies across ROs. While models are useful to test biological and ecological hypotheses, they should always be informed by empirical knowledge. Throughout the report, we highlight where synergies and efficiencies exist, especially where empirical studies would help improve certainty in model predictions.

4.1. Research Opportunities leading to better parameterisation of current population modelling approaches and improved understanding of wider context of kittiwake population dynamics

RO3.1 Use of large-scale strategic modelling approaches to better understand kittiwake meta-population dynamics and estimate connectivity among colonies

Evidence need / Rationale for doing this RO

Many SPAs with kittiwake interest features have Conservation Objectives of maintaining or restoring populations. Therefore, understanding the extent to which immigration and emigration play an important role in maintaining population size and persistence at the scale of individual colonies and more widely is of critical importance. While some tracking and ringing studies at a small number of colonies in the UK and Norway have provided useful insights on the potential spatial scale of dispersal movements, uncertainty remains around the frequency of dispersing individuals, and how dispersing rates vary with distances to the nearest colonies, and over time (due to e.g. changes in colonies' productivity), particularly for the colonies in north-east England and east Scotland. In other words, is there enough immigration going on to supplement a colony that has poor breeding success? This is a key question for kittiwake colonies where consenting risk is high.

There is an overall lack of empirical estimation of movement rates for UK kittiwake colonies; therefore, here it is proposed to use an existing meta-population modelling framework ("Miller model"; see below) to derive estimates of the strength of connectivity between colonies and infer its relative importance in maintaining kittiwake populations.

This RO will help address two of the three KG3 high-level objectives by (1) providing evidence for better parameterising current PVAs and (2) providing wider context to current PVAs.

Work already underway

As part of her PhD thesis, Julie Miller has developed a meta-population model (hereafter "Miller model") for 84 kittiwake colonies in the Shetland Region, including Fair Isle. This is a state-space model that integrates information from both field observations (i.e. colony counts, productivity) and modelled demographic processes, and can impute (i.e. interpolate and forecast) population numbers and estimate critical parameters. Such parameters include the strength of density dependence, the effect of environmental drivers, the influence of local density in juvenile dispersal and the implicit connectivity between colonies as a function of distance between colonies and the arrangement of the entire colony network. Therefore, the model captures both intrinsic and extrinsic regulatory process at the local and regional scale and allows the quantitative apportioning of importance between these important processes.

Work required
This RO can be broken down into four sub-ROs. The proposed modelling approach will be developed as part of an adaptive management framework, so that as new empirical data become available for any colonies or regions, over any period of time (even a one-off survival estimate), they can be incorporated into the model, enabling model predictions to be refined and improved.

RO3.1a Application of the model in UK/regional context using currently available data

A first objective is to estimate the strength of connectivity among kittiwake colonies (accounting for environmental and local density-dependent confounders) in UK areas presenting the highest consenting risk using an existing meta-population modelling framework, which has been developed by Julie Miller and colleagues for Shetland kittiwake colonies. The outputs of the meta-population model could then be used to improve confidence in predictions of the trajectory of the colonies of interest under various scenarios of environmental stochasticity and/or offshore wind farm mortality, given the model-derived estimates of connectivity.

To ensure work under this RO is relevant to offshore wind development, regions where impacts of offshore wind farms on kittiwake populations are predicted to be highest (due to overlap between breeding foraging areas and wind farms footprints; e.g. Forth and Tay region, East England) will be prioritised, on the understanding that kittiwake meta-population dynamics are likely to extend over a wider spatial area. In order to address potential data availability and quality issues, the count and demographic data used for robust spatial estimation of movement rates and processes within regions should be a combination of both high-resolution (depth) and spatially expansive (breadth) surveys. It is therefore recommended to combine detailed flagship survey sites (e.g. Isle of May, where long-term series of breeding numbers, productivity and adult survival are available) with less detailed but synoptic surveys (e.g. Seabird Monitoring Programme data where data is more patchy but covers a wider spatial extent) to parameterise the meta-population model and improve its robustness. Following that approach, the model does not necessarily require site-specific empirical estimates of count and key demographic rates for all colonies, as those could be reconstructed using prior knowledge of the relationship among these parameters obtained in other kittiwake colonies.

Focusing only on individual regions (e.g. south-east Scotland, north-east England) assumes that regions are closed to immigration (as the current Shetland model assumes), which, does not seem biologically realistic given the existing empirical evidence. While this constraint could be relaxed by applying the “Miller model” over wider spatial extents, this may be computationally prohibitively demanding (Jason Matthiopoulos, pers. comm.). An alternative approach may be to extend the model in an approximate way, using resolution selectively. Specifically, a typical nested approach would (1) start by developing a coarse meta-population model of connections between regions of particular interest from an offshore wind development perspective (e.g. north-east Scotland, south-east Scotland, north-east England, south-east England), and then (2) increase the detail within regions, so that connectivity between the colonies in the same region is explicitly modelled in detail. Regions should ideally be determined on a biological basis, e.g. by regional patterns in kittiwake productivity (Julie Miller, pers. comm.).

Inclusion of information on connectivity with colonies outside the UK (e.g. Norway, Faroes) in the meta-population model will need to be considered. The proposed nested approach brings more biological realism to the model; it is also interesting both computationally and in terms of data availability: as we move further away from a region of interest, the resolution of the data, and consequently the model, get coarser. Therefore, kittiwake experts and international collaborators from neighbouring countries could be solicited to gain information on movement distances and frequencies, so that an average estimate of connectivity could be derived and integrated into the broader scale model.

RO3.1b Perform model sensitivity analyses to identify which data gaps most strongly affect model performance

Current data might not support reliable outputs on connectivity among colonies as data may be insufficient. We can use the model to identify where current data are insufficient to give reliable predictions. As part of the model outputs, it will be possible to extract and quantify the amount of uncertainty around outputs parameters, such as the strength of connectivity between colonies or predicted change in population size. It would then be envisaged to run sensitivity analyses in order to identify the parameters that have greatest influence over outputs; e.g. if we reduce the amount of variance on data for input parameters X and Y (e.g. adult survival, productivity), how much increase in precision/confidence do we get for the output parameters (e.g. strength of connectivity between colonies)? This will allow us to identify which new empirical data will help the most with improving confidence in estimates of connectivity. Therefore, the model will inform targeted focussed data collection that will lead to better understanding of connectivity and population change.

RO3.1c Undertake targeted empirical data collection as informed by the sensitivity analyses (RO3.1b)

Outputs from sub-RO 3.1b could be used to inform data collection. This would include identifying the demographic data that would have the greatest impact for reducing uncertainty around model outputs, e.g. obtaining data that would provide more accurate estimates of adult survival (e.g. mark-recapture data) could improve confidence in predictions of connectivity between populations. Some of the demographic data could be delivered through a mark-recapture study, e.g. colour-ringing at many colonies (see RO3.3 below). For example, work under this RO3.1c might include deploying more recapture effort at certain colonies to improve recapture rate, leading to more precise estimates of survival and connectivity. Because of the synergies between RO3.1 and RO3.3, we suggest taking forward both ROs in parallel, ensuring the right data is collected in the right way and maximum benefit/information is derived from the data.

RO3.1d Re-run meta-population (RO3.1a) model with new empirical data to generate improved estimates of connectivity

The new empirical data (collected under RO3.1c) could then be used to parameterise the model built under RO3.1a and the model run again. Given the sensitivity analysis (RO3.1b), the new empirical data should lead to reduced uncertainties in model outputs, such as the relative importance of density dependence and connectivity in determining population size at a colony. This final stage (RO3.1d) leads to the production of better estimates of connectivity and density dependence.

In addition, integrating mark-recapture data, for example as obtained through RO3.3 and RO3.4 (described below), into the meta-population model could be clearly advantageous. Taking forward RO3.1 and RO3.3 concurrently would ensure that data collection under RO3.3 is well-informed and delivers the best empirical data to undertake RO3.1d.

Benefits / Key Outcomes

The proposed approach is based on an existing modelling framework; thus, the same model structure and code can be used and applied, meaning model development costs will be much lower than without this existing model. Additionally, the existing model acts as a 'proof of concept', showing that this approach works over a relatively small area (Shetland), thereby greatly increasing confidence that this model can successfully be applied over a larger area (e.g. Britain).

This strategic modelling approach has the merit of being able to estimate connectivity (immigration and emigration rates) between kittiwake colonies where empirical data are lacking. This is made possible thanks to the wealth of kittiwake colony monitoring data in the UK, in particular the long-term time series of count and demographic parameters from some colonies, such as the Isle of May. Using a state-space modelling approach, it will be possible to impute missing data in some colonies or regions by "borrowing" information from data-rich colonies or regions. The integrated approach will allow combining different datasets and sources of information to analyse population data and demographic parameters.

The outputs of this RO will deliver critical information on the strength of connectivity among kittiwake colonies in space and time, its relative importance (compared for example to density dependence) for population persistence of colonies of concern (e.g. Flamborough and Filey Coast SPA, Forth Islands SPA), and hence provide support for the use of either closed or open population models when using PVAs during impact assessments for these colonies.

The "Miller model" would also allow estimation of the intrinsic growth rate of different colonies and enable that to be linked to environmental fluctuations and/or covariates such as movement rates or density dependence. In other words, it will allow identification of colonies that operate as "source" and "sink" populations at a given point in time. This will help anticipate the potential consequences of changes at other colonies on the focal SPA populations such as Flamborough and Filey Coast SPA. For example, if the Flamborough and Filey Coast SPA is a sink population, we would be able to identify the source population(s) and anticipate what would happen if these sources stopped exporting birds.

This RO will therefore provide evidence that will assist with understanding the wider population context in which individual colonies sit, thereby assisting with bringing greater biological realism to current PVA modelling approaches, which assume closed populations.

An important benefit of this RO is that it will help identify critical data gaps and will inform empirical data collection to ensure the most useful and relevant data are collected for improving confidence in the metapopulation model predictions (as e.g. per RO3.3c-d). In addition, obtaining estimates of the strength of connectivity between colonies in a given region will also help target colonies where observation efforts to detect relocations of colour-ringed kittiwakes (as per RO3.3c-d below) should be maximised. There are therefore obvious synergies between RO3.1 and RO3.3. Ideally both RO3.1a and RO3.3a-b could be done in parallel; RO3.1b could then help target effort in RO3.3c-d, and results from RO3.3c-d could be used to update the meta-population model (RO3.1d).

Finally, the outputs of this work (e.g. estimation of connectivity rates between colonies of interest) could be directly incorporated into an online PVA tool that has been recently developed. The results of this RO will permit more biological realism to be added to the current PVA tool, thereby improving confidence in PVA predictions (see RO3.2 below).

Risks / Inter-dependencies

The proposed modelling framework has already been developed and tested on kittiwake colonies in Shetland. Expertise also exists among academics in the UK, Europe and US to build, parameterise and interpret these complex models. This means that risks around successful model development are low.

The Seabird Monitoring Programme (SMP) provides annual count and demographic data for many kittiwake colonies around Britain and Ireland. However, using SMP data in the metapopulations may be challenging in terms of (1) obtaining empirical estimates of critical demographic parameters and (2) computational power:

(1) Across UK kittiwake colonies, there are still some significant gaps and data issues even with the SMP count and productivity data. To address data gap issues, it is proposed to select colonies where good annual counts and both survival and productivity data exist (e.g. Isle of May) and learn from them to quantify the relationship amongst demographic rates, and between those rates and populations numbers (as done in the "Miller model"). It will then be possible to introduce some strong relationships between colonies in the model by assuming that other colonies cannot vary beyond a certain amount. This will provide reconstruction of survival and productivity time-series where data are not available and better estimation of these demographic parameters where data are available. The same logic applies to when population count time-series are truncated. One example of how this can be done in general (i.e. not necessarily in population models) is Horswill *et al.* (2019).

(2) Computational power will ultimately dictate what can realistically be done within a relatively short time frame. The nested modelling approach suggested above is a good trade-off between biological realism and computational resources. This trade-off will need to be fully considered and discussed with modelling experts before starting the work.

Predicted resources required to deliver this RO

RO3.1a-b The initial model (RO3.1a) can be developed without the need to collect new data, and then subsequently be updated with additional empirical data, as they become available. The sensitivity analysis also does not require any new data collection.

MEDIUM resource requirements (less than one year and less than £100K).
Time required to complete this RO would strongly depend on the overall remit. Below are two scenarios:

- Transfer of existing Shetland model to a new region (e.g. north-east England) and generate predictions of population viability for given mortality rates: **6 months to deliver** for a region the size of Shetland. This includes script writing and debugging, data cleaning and estimating colony-colony distances (about 3 weeks) as well as running models to satisfactory diagnostics (about one month) and running PVA simulations or doing further exploratory work (about 2 months). These estimations depend on the size of the region (spatial extent) as well as the number of colonies included. Defining the spatial extent of a region will be a compromise between ecological relevance (e.g. empirical evidence of the scale of adult kittiwake dispersal suggest movements up to 100km) and the number of possible connections between colonies (i.e. number of colonies within the region).

- Application of meta-population model to UK-wide network, using the nested approach described above: **12 months to deliver**. This is more open-ended and at least 2-3 months of work would be needed to develop the approach. Running times may go into weeks or months, but these only push the delivery time back, not increase the costs of the project.

RO3.1c requires new empirical collection and has higher risk. This could however be combined with RO3.3c-d below.

HIGH resource requirements (a few, and possibly many, years and more than £300K).

RO3.1d would happen at some point in years to come once new empirical data is collected.

LOW resource requirements (less than 6 months and less than £50K), assuming the same model as built under RO3.1a is used. Model improvement/development would increase resource requirements.

RO3.2 Further development of a population modelling tool that assists with assessing population response to changes in mortality or productivity

Evidence need / Rationale for doing this RO

When assessing whether a planned project, e.g. an offshore wind farm, is likely to have an adverse effect on integrity of an interest feature, such as a kittiwake SPA colony, it is necessary to quantify the potential population response to the predicted additional mortality caused by the development. Population models, such as Leslie matrix models, are often used in offshore wind project assessments. Recently, Natural England and JNCC have funded the development of an online population modelling tool, the 'PVA Tool', to improve consistency and transparency in the assessment of potential population level impacts (Information on PVA Tool and Link to online version of PVA Tool). It can also be used to model positive "impacts" on survival and productivity rates and so can be used to explore potential compensatory or conservation measures aimed at increasing population size.

Currently, the tool is designed for use when considering impacts on individual colonies, using either colony-specific on regional demographic data if no colony-specific data are available. Whilst, the current version of the tool has capacity to model multiple "sub-populations" with different demographic rates and different impacts applied, it assumes no immigration or emigration among sub-populations nor other colonies. Given the available evidence suggesting kittiwakes move breeding colonies quite frequently, this assumption may not be valid. Therefore, work under this RO would improve the biological realism of the PVA Tool, leading to greater confidence in outputs of assessments of impacts from planned offshore wind developments.

This RO will help address the second KG3 high-level objective by providing wider context to current PVAs.

Work required

The objective of this RO is to add additional functionality to the PVA Tool, specifically a meta-population function that allows emigration and immigration to be incorporated into the population models. Potentially, other functions that are identified as biologically relevant to kittiwake populations in the UK could be added, e.g. different forms of density dependence where evidence supports it.

This would require:

- A review of potential additional functionality that should be added to the PVA Tool. This should be informed by existing evidence and new evidence arising from other ROs, e.g. the scope for metapopulation functions should be informed by new evidence arising from RO3.1;
- Agreement on which functionality to add and what form/structure it should take. There will be a trade-off between biological realism, which is inevitably highly complex, and

developing a simple transparent model, as well as constraints in terms of data availability. This should be resolved in a way that is most likely to reduce consent risk;

- Model development. This requires advanced modelling and programming skills in R and in Shiny;
- Model testing. Finally, the model changes and improvements require testing to ensure any bugs are removed and the tool performs well.

Benefits / Key Outcomes

This RO will enable those undertaking assessments of the population level consequences of predicted impacts (including evaluation of management, mitigation and compensatory options) to use an updated PVA modelling tool with functionality to model potential population responses with greater biological realism and informed by current evidence. This will lead to increased confidence in assessments.

Risks / Inter-dependencies

The PVA Tool is already available on-line and being used in assessments so risks are low in terms of model development. Evidence on what form the additional functionality should take is currently lacking, e.g. when building meta-population functionality into the model, the extent of connectivity between populations, which age classes it applies to, whether it is a function of colony distance or population size, *etc*. is not currently known. Functionality could be added in a way that allows implementation to be modified as new evidence comes to light.

Predicted resources required to deliver this RO

This RO does not require any new empirical data collection. It requires expertise in population modelling, seabird population dynamics, programming in R and Shiny. These skills, although specialist, are available from several providers in the UK, e.g. CEH, BioSS. Once the form and structure of additional functionality is agreed, implementing the changes should not be too demanding or time consuming.

MEDIUM resource requirements (less than £100K, 6 months to deliver).

RO3.3 Strategic mark-recapture studies to improve empirical estimates of dispersal and survival

Evidence need / Rationale for doing this RO

There are many more empirical data on some demographic rates than others. For kittiwakes, productivity and breeding population size are monitored relatively frequently and, therefore, many population-specific estimates of these demographic rates exist. By contrast, there have been very few attempts to quantify kittiwake survival rates for adults, immatures and juveniles and there is considerable uncertainty around these demographic rates (Horswill *et al.*, in review). Information is also lacking on where new recruits and adults disperse to, and how age at first breeding may vary in relation to local conditions. Age of first breeding is very flexible in long-lived species and is also difficult to monitor; yet it can have a significant influence on rate of population growth. First breeding can occur at a younger age in declining populations, and thus be a mechanism by which compensatory density-dependent demographic processes can bring about an increase in population growth rate.

Better estimates of demographic and connectivity parameters are needed to parameterise PVA models and meta-population models (as described in RO3.1c and RO3.2). This RO will help address the first two KG3 high-level objectives by (1) providing evidence for better parameterisation of current PVAs and (2) providing wider context and more biological realism to current PVA approaches.

Colour ringing, and other mark-recapture methods, are useful monitoring approaches for estimating dispersal distances and, with sufficient re-sightings of marked individuals, directions and rates of dispersal as well as survival rates. If chicks are marked, recruitment locations as well as age at first breeding could be inferred from re-sightings in relation to spatial and temporal variation in carrying capacity but requires a comprehensive re-sighting effort at a representative sample of recruitment colonies.

Colour-ringing is easily implemented at colonies where kittiwake nests are accessible, and not expensive if volunteers are involved to collect relocation data. Each captured and “marked” individual is equipped with a colour ring that has a unique combination of numbers and/or letters and can be seen at a distance, enabling that individual to be identified without recapturing the bird. Re-sighting a “marked” bird confirms it has survived since the last encounter, provides information on its location at a particular time of year, and the distance travelled from the previous site where it was encountered. With a more comprehensive protocol, it is also possible to estimate its breeding status if seen at a colony. If a sufficient proportion of marked birds are re-sighted frequently enough, it will be possible to distinguish between emigration and mortality (i.e. if a bird is not seen, is it dead or has it left the colony?), as commonly implemented in Capture-Mark-Recapture models. A large-scale network of colour-ringing and re-sighting sites will therefore help with obtaining better empirical evidence of both immigration and emigration rates and broaden the number of survival studies which are currently very few.

As immature birds can suffer high mortality rates during the autumn and winter months, the number of colour-ringed chicks in a given area should be large enough to compensate for a relatively low re-sighting probability. There is therefore a need for assessing the feasibility of a high-effort colour-ringing programme of kittiwake chicks to obtain robust estimates of survival rates of immature birds, as well as the age at which they recruit and where. There is also a need for a feasibility study on re-sighting at potential emigration colonies as significant effort would be required (see Coulson 2011).

As well as colour-ringing, other mark-recapture systems include fitting a very small tag to a kittiwake, which can be detected by a network of receiver stations. These receivers can identify individual kittiwakes, providing similar information to colour-ringing studies. Resources required to deploy receivers at a sufficient number of locations to obtain desired data would need to be assessed as part of the feasibility review.

Work already underway

The Retrapping Adults for Survival (RAS) scheme is a citizen-science project within the BTO ringing scheme that encourages all bird ringers to get involved in collecting information on bird survival rates, including seabirds (https://www.bto.org/our-science/projects/ringing/surveys/ras/taking-part/scheme-downloads). A mark-resighting study based on colour rings is already in place for the Isle of May kittiwake colony, and funding has just been acquired to undertake colour-ringing on Inchkeith (Danni Thompson, pers. comm.). In addition, the RSPB have recently set up a kittiwake colour-ringing project - as a new RAS - at the Flamborough and Filey Coast SPA (with 51 colour-ringed adult birds in 2018 and a significant number of re-sightings in 2019, plus an additional 60 new colour-ringed birds in 2019), which could feed into and inform this RO.

The BTO has published a report that reviews historic and existing seabird projects registered in the BTO’s RAS network (up to 2016) and performed a power analysis to evaluate the performance of these projects, in particular how different levels of field effort may impact the ability to estimate adult survival rates (Horswill *et al.* 2016b). The report also looked at the motivations and challenges associated with citizen-science ringing and re-sighting projects. This could form the basis of the review work proposed as part of RO3.3a.

Work required
The work required as part of this RO is composed of two related units: RO3.3a-b will assess the feasibility of implementing a large-scale coordinated mark-recapture programme for kittiwakes breeding along the North Sea coast; RO3.3c-d will implement the mark-recapture programme based on the results and recommendations derived from RO3.3a-b. While RO3.3a-b. could be undertaken as a stand-alone piece of work, undertaking RO3.3c-d. requires completing RO3.3a-b first. Note that there are also synergies with RO2.3 ("Strategic (non-GPS) tracking. Feasibility study") and RO3.1, above. RO2.3 comprises a feasibility study of deploying a large-scale mark-recapture system for obtaining novel empirical data on which SPAs birds using OWF have come from, as well as demographic data. A scope of works has been drafted for RO2.3 that incorporates much of the work suggested below for RO3.3. Whilst there are many similarities between RO3.1c above and RO3.3, RO3.1c might require use of other methods, besides mark-recapture, to obtain all the required demographic data. However, undertaking RO3.1a-b will help greatly with prioritising and ensuring effective data collection under RO3.3.

RO3.3a Feasibility of a coordinated large-scale mark-recapture programme of adult kittiwakes: desk-based review
First, a desk-based review of existing kittiwake colour ringing studies in the North East Atlantic will be required to help target areas where additional survey effort is most needed.

The review will need to cover the following points:

- Locate active and non-active colour-ringing kittiwake studies in Britain, Ireland, Norway and Faroe Islands, as well as upcoming programmes in the UK;
- Has the re-sighting rate of adults been estimated?
- What are the lessons learnt from these programmes? What are the motivations and barriers? Sending questionnaires to volunteer ringing groups should be considered.
- Which mark-recapture systems would be most effective for obtaining desired data?
- How much effort (in terms of number of marked birds per year, re-sighting rate) would be needed to obtain robust estimates? Where and when would that effort need to be deployed within the network of colonies monitored? Outputs of the strategic meta-population model (i.e. connectivity strength between colonies; as described in RO3.1) would help identify where observation effort should be focussed to maximise re-sightings. The review will also need to consider whether there is sufficient understanding of mean estimates and uncertainty to allow for a power analysis to be undertaken to establish likely sample sizes (see Horswill *et al*. 2016b).
- Could the required amount of effort be sustained by a coordinated network of volunteers? Would such a project be viable? Would a network of receiver stations work better?
- Is the greatest need driven by areas where we do not know anything, where there is good long-term monitoring of productivity and count data, or by areas where offshore wind impacts are likely to be highest?
- Identify colonies where mark-recapture could be combined with on-going GPS tracking such as St Abbs' Head, Fowlsheugh and Whinnyfold. This would be particularly beneficial as it would allow improved understanding of demographic rates and foraging areas used at sea by individuals. This type of information can facilitate understanding the relationship between prey availability and demographic rates.
- Would there be merit in catching birds at sea? Would this provide useful information on demographic rates?
- Are there any practical constraints with accessing particular colonies or particular sections of cliffs? What are the implications of this for designing studies to derive survival rates, *etc*?

- Can we identify candidate colonies as part of a functional network, where colour ringing could be encouraged based on e.g. site accessibility to both amateur volunteers and professional ringers (ringing and re-sighting likelihood), colony exposure to offshore wind farms, data needs to improve estimates of impacts *etc*?
- What is the cost of implementing one of these schemes and maintaining appropriate recapture rates to ensure reliable estimation of adult survival? (see e.g. Horswill *et al.* 2018)

The feasibility and cost-effectiveness of a large-scale colour-ringing scheme will need to be compared to other means of marking and 're-sighting' a bird for example genetic analyses and automated systems, e.g. MOTUS (https://motus.org/). A desk-based review aiming at assessing the feasibility of a strategic non-GPS tracking may be taken forward under RO2.3 (KG2 report) and thus the findings of RO2.3 could be used to inform the comparison of technologies and their relative cost-effectiveness for addressing critical data needs. RO2.3 and RO3.3a are very similar, with the same technology potentially being used to obtain both data on connectivity between OWF and SPAs (RO2.3) and better demographic data (RO3.3).

Ideally, RO3.1 would be undertaken concurrently with RO3.3, with information from RO3.1b (the sensitivity analysis) being used to inform data collection under RO3.3. The results of RO3.1b would be used to identify the highest priority data to collect which should focus the feasibility review undertaken as part of RO3.3a+b. If RO3.1 and RO3.3 are both undertaken, it will be important to coordinate across both ROs and ensure work is undertaken in the right order to maximise benefit from the two ROs.

The desk-based review would then be followed by a proposal for coordinating a large-scale kittiwake mark-recapture programme. This might include a wide-scale colour-ringing programme as part of a citizen science initiative (i.e. involving both amateur bird watchers and professional ringers). While citizen science programmes can help increasing monitoring effort at lower cost, the resulting data can be challenging to analyse due to limited survey effort, as well as information on survey effort, which is crucial to model observation and detection biases. The feasibility assessment should therefore include a proposal for a robust scientific calibration of citizen science data with detailed study areas and experienced bird watchers, and for estimating variation in survey effort in space, time and among individuals.

RO3.3b Feasibility of a coordinated large-scale mark-recapture programme of immature kittiwakes: desk-based review

This sub-RO will address the same list of questions detailed in RO3.3a, but with a focus on immature survival rates and age at first breeding. In particular:

- How feasible it is to mark chicks, e.g. to colour ring them? How much marking and re-sighting effort (in terms of sample sizes and area covered) would be required to obtain robust survival estimates of immature kittiwakes given juveniles tend to disperse away from their natal colonies?
- What is the cost of implementing one of these schemes and maintaining appropriate recapture rates to ensure reliable estimation of juvenile survival (see e.g. Horswill *et al.* 2018)?

This sub-RO will also include a proposal for deploying juvenile marking at ecologically significant scales.

Estimating juvenile/immature survival and recruitment is a much more challenging task than estimating adult survival. Natal philopatry (birds that fledge from a colony also breeding at that colony when mature) is not high in kittiwakes. Coulson (2011) estimated 91% of female recruits and 63.5% of male recruits are immigrants, i.e. would be arriving from another colony and so would not be marked, unless marking was also happening concurrently at multiple colonies. Thus, to estimate juvenile/immature survival and dispersal/recruitment robustly requires marking and substantial recapture effort across many years at multiple colonies.

RO3.3c Deploying strategic adult kittiwake mark-recapture at multiple colonies, and analyses of re-sighting data

The feasibility assessment described above (RO3.3a), and the associated recommendations, will inform both the strategic deployment and coordination of a large-scale mark-recapture programme of adult kittiwakes. This should be accompanied by the development of some formal guidance to volunteers, if a colour-ringing scheme is deployed, who are undertaking the re-sighting work in order to maximise the benefit of the data collected, as well as on-line information portals on the way the data are being used.

RO3.3d Deploying strategic chick mark-recapture at multiple colonies, and analyses of re-sighting data

The feasibility assessment described above (RO3.3b), and the associated recommendations, will inform both the strategic deployment and coordination of a large-scale mark-recapture programme of kittiwake chicks. As for RO3.3c, if a colour-ringing scheme is used, this should be accompanied by the development of some formal guidance to volunteers who are undertaking the re-sighting work in order to maximise the benefit of the data collected, as well as on-line information portals on the way the data are being used.

For both RO3.3c and RO3.3d, the following data analyses can be envisaged:

- Analyses of re-sightings as implemented in capture-mark-recapture models to estimate apparent survival rates, and if possible, distinguish between survival and emigration;
- Empirical estimates of survival rates could then be integrated into the state-space meta-population model (as described in RO3.1) to refine survival times-series and improve model predictions;
- Analyses of movement distances, directions and frequency, based on re-sightings within the network of monitored colonies, to better characterise connectivity between colonies;
- With regards to ringing data and connectivity, it is important to note that what we observe in the relocation records is the combined result of dispersal behaviour and density-dependent effects. While the former is what we are really interested in quantifying, the latter is absolutely context-dependent. For example, while a colony can seem to operate as a sink because of the observed net migration from other colonies, the relationship between colonies will change dynamically as density affects the decisions of individuals. Therefore, ideally, the ringing data should be integrated into an analysis of population dynamics directly, not analysed separately. This means that we need to keep a very close exchange between the ringing data and the population modelling (as per e.g. RO3.1).

Benefits / Key outcomes

A long-term, coordinated network of regularly monitored colonies with multiple marked individuals would have the potential to deliver estimates of kittiwake natal and breeding dispersal between colonies, juvenile survival, age at first breeding and adult survival rates. If chicks are marked too and can be re-sighted, additional information will be acquired on survival rates of immatures, age at first breeding, and information on where new recruitments tend to occur. In addition, a coordinated high-effort mark-recapture programme will help distinguishing between emigration and mortality. Overall, this RO would contribute to reducing uncertainty around current PVA modelling approaches through obtaining better empirical evidence of critical demographic rates with which to parameterise PVA models. New empirical data acquired on connectivity and demographic rates through this mark-recapture study could then be used to update the parameterisation of the strategic meta-population model (as per RO3.1d) to refine estimates, as new data become available. This work will build on the outputs of the review work published by the BTO assessing the performance of RAS seabird projects for estimating adult survival rates (Horswill *et al.* 2016b).

This RO would also benefit from the findings of Cook *et al*. (2019), who performed a power analysis of Seabird Monitoring Programme data and provided recommendations on how to increase the power of the monitoring data to detect population-level changes that may be associated with offshore wind farms.

Colour ringing could also be combined with other technology, such as passive detection systems (see RO2.3 in Black & Ruffino 2019), high-accuracy GPS tracking (see RO1.2. in Black *et al.* 2019) or genetic analyses, to improve estimates of survival and dispersal rates at colonies of interest (e.g. Isle of May NNR and Flamborough & Filey Coast SPA). A desk-based review aiming at assessing the feasibility of strategic non-GPS tracking under RO2.3 (Black & Ruffino 2019) could form the basis of RO3.3a-b since the technology used to obtain data to address both RO2.3 and RO3.3 is potentially the same.

Risks / Inter-dependencies

The success of the second stage of this RO (deploying mark-recapture at large scales; RO3.3c-d) is dependent on a strong coordinated strategic overview of the marking programme. For a colour-ringing scheme this would include incentivising volunteers, directing professional effort to areas where volunteers cannot access, managing data collection, data analysis *etc*. The desk-based reviews (RO3.3a-b) would assess both the benefits and risks of deploying mark-recapture on adults and chicks at ecologically meaningful scales and will lay out the fundamental requirements for a successful programme.

Long-term colour-ringing of adult kittiwakes has been successfully deployed in several areas, such as Norway, Scotland, England, Wales, Northern Ireland and France (see http://cr-birding.org/nl/taxonomy/term/2445). Colour-ringing is a simple method and there are lots of keen bird watchers in the UK who would be pleased to contribute data; thus it is likely that a large-scale citizen-science colour-ringing programme deployed in key regions of interest along the UK coast would be technically feasible. That said, it is important to realise that being able to estimate robust survival rates through a mark-recapture study using colour rings is a huge undertaking, particularly if juvenile survival is targeted, requiring many years of substantial effort to search for marked birds. The deployment of marks (e.g. colour rings) is the cheap and easy part of a mark-recapture study; the resource-demanding part is the effort over many years required to obtain a sufficient number of re-sightings of marked birds to usefully estimate survival and connectivity. Data from the RSPB colour-ringing project at Flamborough and Filey Coast SPA have revealed however an adult re-sighting rate of 88% (n=51 adult kittiwakes ringed) at the colony the following year (which provides information on survival, although this alone does not provide any information on the movements of these birds between successive breeding seasons). The scale of deployment and resources required to obtain useful demographic data of sufficient quality/precision will be fully evaluated during RO3.3a-b.

To really be successful and unbiased and to collect data across the kittiwake meta-population, RO3.3d would need to be deployed at substantial scale. This would be a very large and ambitious undertaking.

Predicted resources required to deliver this RO

RO3.3a-b are two desk-based studies that could be completed as a single piece of work. This RO covers the same scope and addresses similar questions as RO2.3. RO2.3. is a review of marking and re-sighting birds, using technologies that include colour-ringing and receiver arrays, to inform connectivity and demographic rates. The Scope of Works drafted for RO2.3 has been written to ensure RO3.3a-b would also be covered, i.e. if the RO2.3 is taken forwards, there would be no need to undertake RO3.3a-b.

For undertaking RO3.3a-b, experience with monitoring kittiwake colonies, colour-ringing kittiwakes and delivering citizen science projects would be required. Expertise in processing and interpreting mark-recapture data would be important in order to be able to estimate data requirements and effort to provide robust estimations of survival rates.

MEDIUM resource requirements for RO3.3a+b (less than £150K, 12 months to deliver).

RO3.3c requires large-scale deployment of a mark-recapture system, high re-sighting effort, data processing and analysis. One advantage of colour-ringing is that colour rings are cheap (ca. 2 GPB per bird + ca. 500 GPB for ringing equipment) and can be deployed over multiple colonies. Intensive field work and equipment (e.g. boats) may however be required to access kittiwake nests and capture kittiwakes, but the technique is available as it is routinely done in some colonies e.g. on the Isle of May and at Flamborough and Filey Coast SPA. Such a large-scale initiative would be appealing to lots of keen bird watchers, and hence has the potential to provide large amounts of re-sighting data at relatively low cost. Most of the resources would be required for ringing birds every year, whereas most of the re-sightings can be made by volunteers and will thus be less resource intensive. Resources will also be required for the analyses of re-sighting data. As an indication, the BTO review report (Horswill *et al.* 2016b) has indicated that the annual costs of undertaking seabird RAS projects could range from under £100 for projects that did not require boat travel, to £6,000 when access required greater logistical support. Colour-ringing kittiwakes at a colony that does not require a boat may require about two months of staff time per year. The accuracy of the estimated survival rates will be dependent on both ringing and re-sighting efforts. For example, a programme running over five consecutive years may provide reasonably good adult survival estimates if at least 200 new adult individuals are ringed each year and re-sighting rate is more than 50% (Horswill *et al.* 2016b). Re-sighting of colour-ringed kittiwakes may also be challenging if birds are nesting in locations that are not easily observed. This would then require a large amount of re-sighting effort across many years to obtain sufficient data on recapture probability of marked birds.

Colour-ringing data from Bempton Cliffs suggest that re-sighting rates of adults can be higher than 50% after one year but these are re-sightings at the same colony. A lot more effort would be required to relocate ringed birds at other colonies. Thus, obtaining robust adult survival rates will require a lot of re-sighting effort. This effort is currently unknown but will be determined by the feasibility review (RO3.3a).

HIGH resource requirements (minimum 5-10 years, minimum £200K per year).

RO3.3d Obtaining robust estimates of survival rates, as well as age at first breeding, will require considerable re-sighting effort since immatures tend to disperse away from their natal colonies. Furthermore, many juveniles and immatures will die during the years before they return to a colony to breed. Thus, a very large number of chicks would need to be marked and recapture effort deployed for many years across many colonies. This effort is currently unknown but will be determined by the feasibility review (RO3.3b). There are likely to be synergies and efficiencies if RO3.3c is undertaken alongside RO3.3d. However, there may be a need to work at different colonies to address the different ecological questions (e.g. understanding adult survival compared with understanding where juveniles recruit).

Additionally, catching and marking adults and chicks requires a different approach and it is unlikely it would be possible at the same nest. Re-sighting of marked individuals can be done irrespective of whether an individual was marked as an adult or chick and so a single deployment of recapture effort would be effective for both RO3.3c and d. However, this assumes again, that it is possible to work at the same colonies to address the different ecological questions.

HIGH resource requirements (minimum 6-10+ years, more than £200K per year).

RO3.4 Reconstructing adult survival rates for populations where empirical estimates are lacking

Evidence need / Rationale for doing this RO
We currently have very good information on breeding success at kittiwake colonies in the UK. However, information on survival rates is lacking due to the logistical and financial demands associated with conducting mark-recapture studies necessary to estimate rates of survival. Currently, survival information is limited to a few intensively monitored colonies. Jason Matthiopoulos and Cat Horswill have developed a Bayesian hierarchical approach that reconstructs population-specific demographic profiles in data limited scenarios. This method has been applied to tunas (Horswill *et al.* 2019) and the analysis could easily be adapted to predict population specific values of adult survival for Black-legged kittiwakes at a national scale.

Work already underway
See published paper by Horswill *et al*. (2019) in *Journal of Applied Ecology*.

Work required
The work would involve collating data on kittiwake breeding success from the various colonies (SMP database) and refitting the model constructed by Horswill *et al*. (2019) to estimate kittiwake annual survival.

Benefits / Key outcomes
The imputed values of population-specific adult survival would be more robust than using surrogate data (e.g. annual averages) in PVA models. However, it is important to note that under current PVA approaches, particularly when using metrics such as counterfactual of population size (CPS) to assess population response to additional wind farm mortality, improved estimates of survival would not bring any substantial increase in certainty to model predictions. This is because metrics such as CPS are robust to inaccuracies in survival rates (Cook & Robinson 2016), which is of substantial benefit when undertaking PVA in data-poor scenarios.

The imputed values would also provide information that would be useful for setting the prior distributions for adult survival rates in the model outlined in RO3.1. Performing both RO3.1a and RO3.4 in parallel could be advantageous.

Risks / Inter-dependencies
The data to inform this modelling approach are already available in the SMP database. Also, the modelling approach has already been developed (Horswill *et al.* 2019). Therefore, risks and dependencies for this RO are low.

Predicted resources required to deliver this RO
This is a desk-based computational analysis based on an existing model. Expertise is widely available from UK providers, such as University of Glasgow, CEH and BioSS.

LOW resource requirements (less than one year and less than £100K).

RO3.5 Estimating the form and strength of compensatory density-dependence in kittiwake population dynamics at different spatial scales

Evidence need / Rationale for doing this RO

One contentious issue when building PVA models for use in impact assessments is consideration of whether or not to include a density-dependent or independent function. The presence or absence, as well as the strength of a density dependent function in a PVA model will strongly determine the predicted population response to offshore wind farm mortality, with population response ranging from maintaining population size to substantial decline. While a recent review of the literature revealed that compensatory density dependence can operate in seabird populations, including kittiwakes (Horswill *et al.* 2017), empirical evidence is often lacking for specific colonies for which we are trying to assess the impact of offshore wind mortality. In particular, there is a lack of empirical evaluation of the form and strength of compensatory density dependence and we do not know how these regulatory processes can change across spatial scales.

This RO will help address the second and third KG3 high-level objectives by (1) providing empirical evidence for the inclusion or exclusion of density dependent functions in PVAs and (2) providing biological realism and wider context to current PVAs.

It is proposed to break down this RO into three parts:

- RO3.5a is a critical assessment of the available kittiwake colony data that will inform both RO3.5b and RO3.5c;
- RO3.5b and RO3.5c are two independent modelling approaches; the latter being more biologically realistic but also more computationally and resource demanding. None of these two sub-ROs are dependent on the outputs of one another, and hence could be addressed independently.

Work already underway

The Seabird Monitoring Programme (SMP) has information on productivity and abundance at different kittiwake colonies around Britain.

CEH has undertaken work to look for empirical evidence of density dependence in a range of seabirds using the SMP data (counts only). As part of that work, Ricker models were used to look for evidence for an effect of population size at different lags on population growth rates, and this allowed to detect compensatory density dependence in approximately 1/3 of the 36 kittiwake colonies tested (Kate Searle pers. comm.; paper in progress). However, as this approach estimated an effect of density dependence on population growth rate, it is not directly useful for PVAs, which typically use demographics rates, so there is a need to identify impacts of density on productivity and survival.

Work from the Matthiopoulos group (first author is Jana Jeglinski) has considered three density-dependent population processes in the meta-population time-series of northern gannets (*Morus bassanus*): i) local density dependence (pertaining to availability of suitable nesting locations on the colony), ii) regional density dependence (pertaining to marine resources experienced by groups of colonies), and iii) global density dependence (pertaining to density-driven relocation decisions of juvenile gannets across the network of colonies). Local density dependence was driven by strong priors provided by experts who have worked on the individual colonies. All three of these processes are probably essential for a meta-population model to explain the available data and to provide biologically realistic predictions into the future. Models with no density dependence at any one of these levels may have difficulty to converge, as a result of strong discrepancy between model and reality. In their work, even removing density-dependent connectivity between colonies leads to difficulties. The gannet data were characterised by extensive lack of data and therefore required considerable imputation. Some of the populations were also affected by spatially and temporally varying levels of anthropogenic mortality (harvesting), so they offered a valuable test for counterfactual metrics (what has happened vs will happen upon being released from harvesting). In addition to this minimal set of modelling features, it appears that useful extensions to such models could include i) hierarchical (i.e. distance-dependent) modelling of the similarity of regional density dependence experienced by different colonies, ii) distance-dependent as well as density-dependent relocation at dispersal (this feature is already included in Miller's meta-population model), and iii) dynamic carrying capacities to reflect temporal changes in prey availability and breeding habitat quality. The analysis for this paper is finished and the manuscript is at first draft stage, with submission expected by June 2020.

Work required

RO3.5a Critical review of existing kittiwake colony data

A precursor of the modelling work proposed below in RO3.5b and RO3.5c is a critical review of the colony data available, which will inform the collation of a dataset that will be appropriate for these modelling exercises, and hence help detect and inform assessments of density dependence. The parameters for which critical data are needed are breeding numbers, nest density, population growth rate and productivity. Ideally, these data would need to be available across spatial scales (e.g. plot, colony, SPA population, region).

RO3.5b Measuring compensatory density dependence at different scales using the Seabird Monitoring Programme data

This RO would involve a meta-analysis of the available data in order to examine whether a universal functional shape of density dependence exists (e.g. Horswill *et al.* 2017). This work would involve comparing abundance, nest density, population growth rate and productivity at colonies monitored by the SMP to try and detect patterns of density dependence. By looking at these demographic parameters at different spatial scales, e.g. subplot, colony, SPA, regional scale, it will be possible to search for evidence of density-dependent regulation of population growth rate, productivity and survival in relation to population size and density (at different time lags) and relate these processes to candidate drivers (e.g. nest site vs. prey availability). Using a state-space population model for colonies that have both count and productivity data (and ideally survival rates) will allow imputation of missing data (e.g. when time-series are imperfect).

Depending on data availability and the results of RO3.5a, this model could be applied to areas of interest from an offshore wind development perspective, such as Flamborough and Filey Coast SPA, and thus address the question of whether compensatory density dependence is operating at these colonies and at what scale, and what forms and shapes the relationships may take.

RO3.5c Measuring compensatory density-dependence by modelling carrying capacity

As carrying capacity is difficult to measure in the field, a common approach is to estimate it using long-term time series of count data. While previous studies have considered carrying capacity as a single upper threshold limiting population growth, it can operate at both regional (food) and local (breeding site) scales, with different processes involved (e.g. Jeglinski *et al*., in progress). This is particularly relevant to seabirds, which use both terrestrial (colony) and marine (fish prey) environments. This means that to accurately model kittiwake population regulation, we need to consider at least two carrying capacities.

However, differential effects of overarching trends in environmental conditions, regional differences in food availability and the quality of the colony itself may be difficult to tease apart, due to a combination of lack of empirical data and appropriate modelling approaches. Importantly, we do not have a good understanding of the relative importance of local vs. regional carrying capacity, and how together they regulate kittiwake populations. While there is good quantitative evidence supporting regulation of UK breeding populations by regional food availability, the evidence for local regulation via nest site availability is based on anecdotal instances and its relative importance as a population regulatory mechanism needs to be further explored.

With this RO, it is proposed to develop a demographic model that would include two types of carrying capacity (regional vs. local) with population size forced towards carrying capacity through compensatory density-dependent processes. This meta-population model would be applied across all UK kittiwake colonies. Expert elicitation could be used to parameterise local carrying capacity (e.g. breeding site quality) when empirical information is lacking. Data from both large and small colonies, as well as colonies experiencing varying intrinsic population growth rates would be required. This modelling framework is inspired by the work of Jason Matthiopoulos and his team on gannets (Jeglinski *et al*., in progress; see above).

Benefits / Key outcomes

While there is general acceptance of compensatory density dependence in kittiwake population dynamics at a high level, better empirical evidence of these regulation processes in specific colonies or populations of interest is needed to build robust impact assessments.

These three sub-ROs could obtain evidence from empirical data for the strength, form and scale over which compensatory density dependence might operate in areas of interest, for example Isle of May NNR (part of the Forth Islands SPA) or Flamborough and Filey Coast SPA. These modelling exercises will help identify impacts of density on productivity and survival, and not only population growth rates, which is directly relevant to PVA modelling. Therefore, outputs from these sub-ROs would help improve the structure of PVA models currently used in impact assessments as well as provide wider context about the spatial scale at which intrinsic population processes are occurring, which would help with interpreting outputs from current PVA approaches.

Through the critical review of available colony data, RO3.5a will help identify critical data gaps and thus inform future studies and data collection.

RO3.5b and RO3.5c will also provide some insight on the relative importance of local (nest site availability) vs. regional (prey availability) on kittiwake population dynamics. This is of great importance for targeting conservation measures.

Risks / Inter-dependencies

RO3.5a This sub-RO is a desk-based review of the SMP data. There are no foreseen significant risks.

RO3.5b The regional meta-analysis requires time-series of count and demographic data but these are available through the SMP database. There may be colonies which present gaps in time-series count data; however, this issue could be tackled by using state-space models, which allow data imputation. Expertise exists in the UK from several providers (e.g. Glasgow University, CEH, BioSS) with using these sorts of models and data.

RO3.5c Overall, this work would be computationally demanding (each model fit takes 8 days of computing time and we may need to explore >100 such experiments to arrive at a stable model version; Jason Matthiopoulos, pers. comm.). It would also require extensive time-series data for each colony, to understand local characteristics of carrying capacity, or alternatively highly informative expert opinions. Some of the risks of this RO will be reduced by undertaking a critical assessment of the data (demographic rates) currently available (as per RO3.5a). Moreover, some regions may present evidence of local density dependence in all of the colonies in that region. If that is the case, then regional carrying capacity will be non-identifiable. Options to address some of the modelling limitations described above have not been implemented yet, thus the funders should be aware that they are supporting novel untested modelling approaches. For example, there are a lot of unknowns and confounding factors at play here. This work is proposed to be broken down a bit to explore some of these issues before building the model.

Predicted resources required to deliver this RO

RO3.5a
LOW resource requirements (less than 6 months and less than £100K).

RO3.5b
MEDIUM resource requirements (less than one year and less than £150K).

RO3.5c
HIGH resource requirements (more than one year and more than £200K).

RO3.6 Detecting depensation effects by modelling kittiwake population dynamics

Evidence need / Rationale for doing this RO

A review of density dependence found evidence for depensation in some seabird species, e.g. increased predation when colony size was smaller (Horswill *et al.* 2017). The review identified two studies reporting depensatory density dependence in kittiwakes, and this could still be an important mechanism for causing extinction of small and declining populations. Avian predators, such as ravens, sea eagles, great skuas, peregrines and large gulls, are common at kittiwake colonies, particularly at Norwegian and Shetland colonies. Whilst these predators will predate chicks or eggs, they may also take adult kittiwakes if the opportunity presents.

The reason why there is limited evidence of depensation effects in kittiwake populations could be that these effects are difficult to detect, as there are not many colonies that are sufficiently small such that depensation could occur (note that kittiwake colonies in Norway however tend to be much smaller than in the UK and predation is higher). There are also confounding factors at play. For example, social dynamics as well as predation could influence depensatory density dependence, with kittiwakes known to be more likely to move to a new colony if their neighbours have poor breeding success (e.g. Boulinier *et al.* 2008; Ponchon *et al.* 2015). In addition, vulnerability can differ from one colony – or part of a colony – to another depending on breeding habitat quality (individual kittiwakes, with the better quality individuals having better nest sites and the poorer quality individuals being on the edge of the colony); as such depensation could be confounded with centre-edge effects (which are strong in kittiwakes; e.g. Coulson 2011).

This RO will help address the first KG3 high-level objective by providing empirical evidence of the type of density dependence to include in current PVA approaches. Consideration of depensatory density dependence is of particular importance when modelling potential impacts from offshore wind development. This is because there may be a tipping point when a population is pushed below a threshold population size by wind farm mortality, and once below that point, depensatory density dependence drives the population to extinction. Identifying and avoiding that tipping point is critical to ensure SPA Conservation Objectives are met.

Work already underway

There are possibly a few candidate colonies in Shetland and southern England where depensatory density dependence may operate or have operated in the past. Some of these colonies have undergone declines and colony abandonment in some cases. There is evidence that while initial colony decline may have resulted from wider scale reductions in productivity, subsequent breeding failure and abandonment seem to have resulted from local small-scale events like predation and disturbance.

Some monitoring data may also be available from newly founded colonies in the north-east coast of England (e.g. Coquet; Tyne), including information on philopatry (e.g. see Coulson 2011), but this will need to be further researched.

Meta-population models that include density dependent terms have already been developed and tested for kittiwakes (Shetland region; Miller *et al*. in progress, see RO3.1) and gannets (UK wide; Jeglinski *et al*., in progress, see RO3.5).

As for the UK-wide gannet model (Jeglinski *et al*. in progress), a kittiwake model could include useful additions such as i) depensatory density dependence (Allee effects) for newly founded colonies, ii) different levels of depensation for small but increasing, versus small but decreasing colonies, iii) hierarchical (i.e. distance dependent) modelling of the similarity of regional density dependence experienced by different colonies, and iv) distance-dependent as well as density-dependent relocation at dispersal (this feature is already included in the “Miller model”, RO3.1).

Work required
This RO would require first undertaking a desk-based assessment of the kittiwake colony monitoring data available (RO3.6a) in order to assess the feasibility of measuring the strength of these effects on intrinsic population growth rates using a population model (RO3.6b).

RO3.6a Desk-based review of kittiwake monitoring data

A precursor of the modelling work is a critical review of the current and historic kittiwake colony monitoring data in the UK, but also in northern countries such as Norway, where field observations suggest that depensation may occur. This review work will aim at identifying those colonies which are declining or have undergone a sharp decline in the past that could be attributed to predation. This work will build on the literature review of Horswill *et al*. (2017) and will also include a search for monitoring data from newly founded colonies (this data could be captured for example by getting hold of long-term time series of population size and demographic rates from the founding time of a colony). There may be a need to contact reserves managers to access data in countries where colony monitoring data is not centralised in a single database (at it is the case in the UK, with the SMP data).

This review will outline the range of population sizes and population growth rates of monitored kittiwake colonies and will identify likely candidate datasets and colonies where depensation effects could be assessed using population modelling.

RO3.6b Modelling depensation effects

Based on the data available (identified in RO3.6a), it is proposed to develop a state-space model that includes a depensatory term (i.e. positive density dependence) to estimate its strength. This has already been done with the “Miller model” (for compensation) and trialled for the “Jeglinski model” (for depensation). Depending on data availability, depensation effects could be assessed using data from one or two types of colonies: 1) declining colonies suffering high levels of mortality from e.g. predation and having reached a critical density threshold, and 2) small size, emerging colonies. In the case of small emerging colonies, the analyses would need to be done in a meta-population context to account for availability of external recruits into emerging colonies.

Benefits / Key outcomes
This RO will obtain evidence from empirical data for the shape of the density dependence relationship in kittiwake populations. Thus, outputs from this RO would inform the structure

of PVAs currently used in impact assessments as well as provide wider context about the spatial scale at which intrinsic population processes are occurring, and hence more confidence in outputs from current PVA approaches.

Using state-space population models for addressing these questions is important here as these sorts of models will allow estimation of intrinsic population growth rates (which is a property that cannot directly be measured) and thus obtaining more certainty in predictions of critical density thresholds.

Importantly, this work will allow identification of ‘tipping points’ in kittiwake colony size/density below which a colony could decline to extinction. A colony might tolerate additional mortality showing only small declines, until this tipping point is reached, when the population then declines to extinction. Identification of this threshold is important in conservation management of kittiwake colonies.

The desk-based assessment (RO3.6a) may be better achieved in conjunction with RO3.5a, as these two sub-ROs are based on a critical review of existing kittiwake colony monitoring data.

Risks / Inter-dependencies
The main risk with this RO is availability of empirical data, which will limit our ability to estimate the effects of depensatory density dependence. Using data from newly founded colonies can help model and detect depensation, but unless there is good data from the founding time of a colony throughout the initial “take-off” phase, depensatory density dependence can prove hard to estimate. Availability of data will be determined by RO3.6a. This RO will use and extend existing modelling approaches. Expertise also exists among academics in the UK, Europe and US to build, parameterise and interpret these complex models. Altogether, this means that risks around model development are low.

This modelling work would require reconstructing historical count data (from SMP and seabird censuses) from colonies in different regions, but this is a standard approach when applying state-space models.

It is worth noting that although the model proposed under RO3.6b will have a similar baseline structure as the “Miller model” (it would be a state-space model with a density-dependent term), these models do not address the same questions or test the same hypotheses. For example, the “Miller model” is built to estimate the strength of connectivity between colonies, while the proposed RO3.6b model will focus on the form and strength of density-dependence. Therefore, it is not proposed to build the RO3.6b model as a direct extension of the “Miller model”. The “Jeglinski model” (on gannets) would represent, on the other hand, a better baseline model, whose functionalities could be extended to incorporate depensation effects.

Predicted resources required to deliver this RO
RO3.6a
LOW resource requirement (less than 6 months, and less than £100K).

RO3.6b
MEDIUM resource requirement (more than 12 months and more than £200K).

RO3.7 Assessing the importance of non-breeding birds in UK kittiwake populations

Evidence need / Rationale for doing this RO
Skipping breeding is relatively common in long-lived and territorial species, and in seabirds and can be driven by multiple factors such as trading-off own productivity against adult

survival, adult senescence or losing a breeding partner. Therefore, populations of seabirds are often characterised by a relatively small ratio of breeders to non-breeders, compared to shorter-lived bird species. As for kittiwakes, an important knowledge gap is the evaluation of the proportion of the pool of adult non-breeders in a population. This is important as non-breeders may be available to compensate for a decrease in adult survival at a colony by recruiting into the colony and using empty nest sites left by previous breeders.

Work already underway
Various datasets exist in the North-East Atlantic that combine geolocator (GLS) tracking data over the life cycle of kittiwakes with monitoring of their breeding status and success at colonies. Ringing data also exist in the UK and other northern countries, where information could be extracted on breeding frequency, if re-sighting effort is high enough.

Work required
Under this RO, it is proposed to conduct a feasibility study and address the following questions: 1) What empirical data are available from for example long-term monitoring of individual movements (e.g. with GLS tags or re-sighting data of ringed birds); 2) Can the available information provide insights on the spatial scale of influence of non-breeders (e.g. where do non-breeders recruit); 3) What additional analyses could be done to estimate the extent of non-breeding in kittiwake populations from available data on population size, breeding success and adult survival, and 4) What additional data would need to be collected to increase robustness of the results.

Benefits / Key outcomes
This RO will increase the knowledge base around the extent of non-breeding by adult kittiwakes in UK populations. This work will help anticipate the ability of kittiwake populations to buffer against additional mortality caused by offshore wind farms, through density-dependent rescue effects (i.e. immigration). This will therefore improve understanding of the wider context in which current typically colony-specific PVA approaches sit.

Risks / Inter-dependencies
Low – this is a desk-based review of existing data. The existing data may be scattered and scarce, but this RO will help direct collection of data where empirical evidence is lacking.

Predicted resources required to deliver this RO
LOW resource requirement (less than 12 months, and less than £100K).

4.2. Research Opportunities focussing on understanding potential kittiwake population response to changes in management of drivers of population change

The following ROs consider drivers of change in kittiwake populations that can be managed, such as commercial fisheries, as well as the wider context in which current PVA approaches sit, e.g. climate change. These ROs will both improve understanding of the wider context of kittiwake population dynamics as well as informing discussions around the potential for possible management measures to achieve desired outcomes.

RO3.8 Examining the ecosystem processes driving the relationship between kittiwake breeding success and sea surface temperature

Evidence need / Rationale for doing this RO
This RO will aim to better understand why some kittiwake colonies are more resilient and others more vulnerable to additional mortality, e.g. from OWF. By contrast to some of the ROs above that look at intrinsic biological mechanisms determining population size at a

colony, this RO looks at extrinsic drivers of change, including climate change and effects of commercial fishing. It will build on previous work that has established a negative relationship between sea surface temperature (SST) and breeding success, which varies between different colonies. The processes underlying this relationship are likely to be related to the availability of the kittiwakes' prey, which is determined by a complex interaction of factors operating in the food-chain, which have so far proved difficult to elucidate. This RO will examine how various environmental and biological factors may have led to variation in breeding success between colonies and within colonies over time. By doing so, we will obtain a better understanding of the processes that affect the breeding performance of this species. This will allow us to better predict the likely future impacts of climate change on kittiwake populations, enabling current PVA predictions to be interpreted in a wider biologically-relevant context, e.g. how is a population likely to respond to climate change over the next decade and how does this compare to predicted offshore wind farm mortality. Additionally, information from this RO will help inform the efficacy of conservation measures, through understanding how kittiwake populations will respond to measures in the presence of a shifting baseline, due to climate change.

Work already underway

The negative relationship between kittiwake breeding success and SST, which was first established by Frederiksen *et al*. (2004), has recently been used to construct an indicator for the UK Marine Strategy (Mitchell *et al.* 2018). The indicator was used to determine if kittiwake breeding success is being driven largely by prevailing climatic conditions or is being impacted by other human pressures (e.g. fishing) or natural factors other than climate warming (e.g. predation, weather). The indicator was developed by Cook *et al*. (2014) and was constructed from breeding success data collected at 22 kittiwake colonies on the North Sea coast of Britain and was assessed annually during 1986–2015. Cook *et al.* (2014) found that breeding success was correlated with SST except at key points in time in certain areas. For instance, breeding success was lower than expected during the late 1980s in Shetland following a crash in the local sandeel stock (Hamer *et al.* 1993; Wright & Bailey 1993) and during the 1990s at colonies in eastern mainland Scotland that were adjacent to an area of high sandeel fishing pressure (Frederiksen *et al.* 2008, 2004). The fishery was closed from 2000 onwards.

Since 2009, breeding success at mainland colonies has been in line with SST, except at Bempton Cliffs and Flamborough Head where it is lower than expected, possibly due to impacts from a sandeel fishery on the nearby Dogger Bank (Carroll *et al.* 2017).
In contrast, at all kittiwake colonies in Orkney and Shetland breeding success has been below that expected from SST since 2001. Many kittiwake colonies in Shetland and Orkney have failed to produce any young in numerous years since 2001 and have experienced the steepest declines in breeding numbers in the UK (JNCC 2020).

It is unclear why kittiwake breeding success has been poorer than expected across all colonies in Orkney and Shetland since the early 2000s. It is unlikely to have been due to fishing pressure, since this was low or even absent due to voluntary bans during this period (ICES 2017). In some years, extreme weather events (e.g. such as heavy-rain washing nests from cliffs) may also have lowered breeding success, but such events are unlikely to have caused such widespread and sustained reductions in breeding success. At some colonies, particularly on Shetland, predation from great skuas is likely to be a major cause of poor breeding success and declines in colony size (Heubeck *et al.* 1999; Votier *et al.* 2004).

Work required

The breeding success/SST relationship will be constructed at the 22 UK North Sea colonies used in the UK kittiwake Breeding Success indicator (Mitchell *et al.* 2018) using methods established by Cook *et al*. (2014). It will use data from the SMP collected since 1986 and be updated with the most recent data.

The RO will examine this geographic variation in the relationship between SST and kittiwake breeding success and the temporal deviation from this relationship at individual colonies. It will do so in the context of spatial and temporal variation in environmental and biological factors. Abiotic factors will include temperature at the seabed as well as the surface, stratification, current circulation and various measures of weather conditions. Biological factors will include indicators of the structure and function of the food chain including primary production, phytoplankton biomass, zooplankton abundance and if possible, data on phenology of zooplankton spawning and larval fish abundance. This RO can also link to RO3.9 by incorporating data on temporal and spatial variation in kittiwake diet during the breeding season.

Benefits / Key outcomes

This RO will improve understanding about the most likely factors affecting kittiwake breeding success across a range of colonies. This will improve our understanding of what determines population size at colonies of relevance to offshore wind development, e.g. it would assist with understanding why breeding success at Flamborough and Filey Coast is lower than would be expected by SST alone and to explore the role of the Dogger Bank fishery on kittiwake productivity at this colony. This insight will help both improve predictions about how these colonies are likely to respond to additional offshore wind mortality as well as better understanding what effect changes in management might have, e.g. closure of certain fisheries.

Risks / Inter-dependencies

Low – all data used in this study are publicly available. The relationships between kittiwake breeding success and SST that underpin this study have already been established by previous work (e.g. Carroll *et al.* 2015; Cook *et al.* 2014; Frederiksen *et al.* 2004; Mitchell *et al.* 2018).

Predicted resources required to deliver this RO

This is a desk-based analysis based on existing code. The work was originally developed by BTO and JNCC, but expertise is widely available from other UK providers.

LOW resource requirements (one year and less than £100K).

RO3.9 Kittiwake diets during the breeding season, and the relationship between prey availability and productivity

Evidence need / Rationale for doing this RO

Food abundance and availability during the breeding season have been shown to strongly influence productivity in kittiwake populations. By better understanding how kittiwakes respond to spatial and temporal variation in food availability, we can predict with more confidence how these populations might respond to commercial fisheries management and climate change. Since these variables strongly determine kittiwake population size and growth rate, they also determine how resilient a population will be to additional mortality, e.g. from offshore wind development.

Better understanding of what breeding kittiwakes eat in different regions, whether their diet can vary between colonies within a region and between sections of a colony, and how it has changed over time at a given colony, would give us insights on the breadth of their diet, their ability to switch prey, and the relative prevalence of sandeels, as well as non-sandeel prey, in their contemporary diet. This is important as the ability to use other non-sandeel prey resources and the consequence of prey switching on demographic rates determines how well kittiwake colonies are likely to tolerate additional mortality, e.g. from OWF, in the future. Predicting their response to changes in prey availability cannot be addressed solely by looking at the relationship between kittiwake productivity and some averaged indices of prey abundance or biomass, as these indices do not necessarily reflect the availability of prey at different periods of the breeding season, including the most energetically-demanding periods. Accounting for timing of breeding and prey is therefore important.

This RO combines desk-based and field studies that will help build confidence in how kittiwake populations are responding to on-going changes in prey availability and thus assess their resilience in the context of declining sandeel stock biomass in the North Sea.

Work already underway

The Marine Ecosystems Research Programme (MERP) has constructed, and continues to populate, a comprehensive time- and spatially-explicit database of diets for ten seabird species (including kittiwakes) in the British Isles (Krystalli *et al.* 2019). This brings together for the first time all the available information about the food resources of these British seabirds. As of March 2020, diet data was available for 17 different colonies spanning from 1963 to 2015 (between one and 17 years of data per colony). Diet samples from regurgitates were also available at Flamborough and Filey Coast SPA that have yet to be processed and analysed. (https://github.com/annakrystalli/seabirddietDB)

Monitoring of kittiwake breeding success is available at a number of colonies in the UK, some with good long-term time-series of count and productivity data (e.g. Isle of May). Thanks to the RSPB FAME and STAR projects, GPS tracking of kittiwakes was undertaken at a total of 22 kittiwake colonies around Britain and Ireland. These data were analysed to predict UK-wide breeding distribution foraging maps (Wakefield *et al.* 2017) as well as SPA-level hotspot maps (Cleasby *et al.* 2018). Further GPS tracking of breeding kittiwakes is currently ongoing at Flamborough and Filey Coast SPA, St Abbs Head SPA, Fowlsheugh SPA and Buchan Ness to Collieston Coast SPA.

Information on fish distribution, abundance and biomass data, including sandeel, sprat and herring, is publicly available from ICES. Monitoring of fish abundance and biomass is also available from Marine Scotland and CEFAS.

Recently, JNCC and SMRU undertook a piece of work that aimed to map the distribution of harbour seal prey species (“calorific maps”), that include Atlantic cod, whiting, European sprat, Atlantic herring and sandeels (Family *Ammodytidae*) in the North Sea (Ransijn *et al.* 2019).

Work required

It is proposed to break down this RO into three parts.

With the two first parts of this RO (RO3.9a-b), it is proposed to explore the regional and temporal patterns of kittiwake prey types and quality in the UK. For example, do breeding kittiwakes prey on different fish species in different UK regions, colonies or sub-colonies? What types of fish are they eating, what age class, size and quality? Is there evidence of prey switching over time? Assessing how diet varies between sections of individual colonies will also give us insights on why kittiwake productivity may differ within an SPA, as it was observed at Flamborough and Filey Coast SPA. RO3.9a is a scoping exercise involving a review of the existing knowledge base and identification of evidence gaps, while RO3.9b involves collecting additional diet information at colonies to fill in these gaps.

RO3.9c aims to assess the relationship between food availability and kittiwake productivity from colonies where more detailed information could be gained by combining diet studies, breeding success monitoring, GPS tracking and prey availability data.

RO3.9a Spatial and temporal assessment of kittiwake diets, foraging distributions and prey distributions during the breeding season: desk-based study

This RO requires reviewing the existing information on kittiwake diet during the breeding season, their foraging distributions and prey distributions in the UK.

The MERP diet database is a valuable resource for sourcing pre-2018 kittiwake diet studies. Under this RO, UK kittiwake experts would also be contacted to find out whether diet information is available from ongoing unpublished studies. It would also be valuable to source any unpublished diet studies, or anecdotal information, on kittiwake diet pre-1985 when sprats were more abundant in the North Sea (by e.g. contacting Mike Harris). The information acquired will be used to assess the current knowledge base and identify critical evidence gaps. For example:

- What types of diet data already exist for kittiwakes, and where? Has prey been identified to species, age and size classes? When during the breeding season has diet data been collected? What are they eating, of what age class and sizes, and where?
- Has prey consumption data been collected or estimated (or is it just proportional diet data)?
- Is there evidence for differences in chick diet composition between UK regions, colonies and sub-colonies? Is there evidence of prey switching over time within colonies or regions?
- How do these diet composition patterns relate to other UK seabird species that have similar foraging strategies? Can we detect common trends in prey switching across species?
- How many years of chick diet data have been collected for each colony? How many samples were collected and from how many individuals per colony per year?
- Do we have a good understanding of contemporary kittiwake diets at colonies where consenting risk is high (e.g. East Caithness Cliffs SPA, Fowlsheugh SPA, Forth Island SPA, Flamborough and Filey Coast SPA)?

The results of this review will identify current gaps in knowledge. In particular, are there any particular areas where consenting risk is high and contemporary information on kittiwake diet during the breeding season is lacking?

As part of this RO, it would also be valuable to review GPS tracking data for breeding kittiwakes in the UK, as well as contacting forage fish experts and sourcing data on UK fish prey abundance and biomass, to address the following questions:

- For those colonies where diet data is available, is there GPS tracking data available to identify where breeding adults were foraging in years when diet information was collected? How many individuals were tracked and how many individuals were analysed for diet? Are the samples representative of the whole colony?
- Is there evidence that kittiwake colonies are using the same foraging areas over the years? Are they travelling further offshore in some areas?
- What is the current distribution of fish prey species? Is abundance/biomass data available for all kittiwakes’ prey types in the North Sea, west coast of Scotland and Irish Sea?
- Can we relate diet and foraging distributions of a particular colony to fish prey abundance and biomass in areas where we know kittiwakes are foraging?

RO3.9b Regional comparison of kittiwake diets during the breeding season: field studies

This sub-RO will involve more detailed field studies at those UK kittiwake colonies with high consenting risk and where contemporary kittiwake diet information is lacking (as identified in

RO3.9a). This could also include colonies in the Irish Sea where several lines of evidence suggest that sandeels may not be an important food source for breeding kittiwakes, therefore informing on the extent of prey switching. Better understanding of what kittiwakes feed on in areas of high consenting risk will help identify relevant fisheries management measures.

Setting up cameras at nests is not appropriate for monitoring kittiwake prey delivery to chicks as chick feeding occurs too quickly and the regurgitate is challenging to identify to prey type from camera observations. Alternative options are to collect prey regurgitates at the nest and collect droppings for genetic analyses. While the former is routinely done in some kittiwake colonies as part of a long-term monitoring of kittiwake diet, the feasibility of analysing DNA in droppings to infer kittiwake diet would need to be assessed. It has been done however on red-throated divers (Kleinschmidt *et al.* 2019). Combining morphological and molecular approaches may be recommended to minimise the limitations of these techniques (Horswill *et al.* 2018).

It is probably not useful to use stable isotope analyses in this instance since this technique will only provide an idea of prey trophic level, as opposed to empirical evidence of adult kittiwakes feeding on sprat, sandeels or other fish species from the same trophic level. Ideally, prey consumption data will include information on prey species, age or size class of prey, and biomass ingested (therefore not just proportional diet data). In addition, using cameras at nests, combined with field observations, will assist with measuring chick provisioning rates, and hence obtain estimates of daily energy intake in relation to types of prey fed to chicks. It is also proposed to assess the extent of diet variation within colonies by simultaneously sampling chick diet in different sections.

RO3.9c Relating prey availability to productivity: desk-based study

This sub-RO will aim at better understanding the relationship between kittiwakes' prey availability during the most energetically-demanding period of the breeding season and productivity. Poor availability of 0-group sandeels during the chick-rearing period may explain why kittiwakes perform poorly, in which case an effective conservation measure should aim at increasing availability of 0-group sandeels during the chick-rearing season in areas where adult kittiwakes are known to forage.

Prey availability during the chick-rearing period will be assessed by obtaining data on fish landings (incl. 1+ and 0 sandeel groups) during that period. Sourcing relevant historic and contemporary landings data will be informed by knowledge of what adults provision their chicks at a given colony and where adult kittiwakes from this colony forage during the chick-rearing season. Chick diet data will be obtained from both historic and contemporary diet studies (as per RO3.9a-b). Knowledge of where kittiwakes are foraging at colonies where diet data is available will be obtained by using existing GPS tracking data, as well as previous research linking colonies with the dependent sandeel populations (Olin *et al.*, in press).

Candidate colonies for this sub-ROs are those where chick diet data is available (with a preference for colonies providing several years of data), as well as GPS tracking and colony productivity data.

Benefits / Key outcomes

These three sub-ROs will improve our understanding of the relative importance of certain types of forage fish for kittiwakes during the breeding season across regions and over time, which will provide insights on the range of relevant measures that could be put in place to compensate for potential additional wind farm mortality.

This work would provide some insights on the ability of kittiwakes to switch prey types in relation to availability, as well as its demographic implications, and therefore their resilience in the context of declining sandeel stock biomass in the North Sea. The findings of these sub-ROs could be directly fed into current advances of PVA modelling approaches, such as the “MSS-funded seabirds-climate change” project led by CEH, which aim to produce better estimates of wind farm effects on future population change in protected seabird populations. This project will incorporate the effects of climate change (through changes in prey availability) on seabird behaviour, demography, abundance and distribution into impact assessments.

This RO could also feed into RO3.8 in terms of examining whether spatial and temporal variation in prey species explains some of the variance in relationships between kittiwake breeding success and abiotic variables (e.g. SST, timing of stratification).

Risks / Inter-dependencies
A key risk of using diet data is that, in general, diet is liable to adapt dynamically to changes in prey availability. This may imply that natural systems are much more buffered from change than is suggested by current data. With this RO, it is proposed to capture diet data from multiple points in time and space, i.e. at different colonies, which will help address the issue and minimise risks.

Another risk is that there are relatively poor fish biomass data for the west coast of Scotland and the Irish Sea, due to the closure of Scottish west coast fisheries. There might be however larval sandeel data from some CEFAS surveys for the Irish Sea; the review (RO3.9a) would investigate this. In areas where there are no data available on fish prey, an alternative option would be to explore options for obtaining live prey abundance and availability data (e.g. by flying a low-flying plane in areas identified as foraging hotspots for kittiwakes), and comparing the fish observed at the surface with the fish found in the regurgitates. However, as doing these surveys will increase the cost of the whole project, a thorough evaluation of the cost and benefits of several alternative means will be required. Sourcing relevant datasets will be facilitated by the availability of an online tool (MERP seabird diet database; unpublished version can be accessed by contacting authors) that compiles seabird diet information, including kittiwakes, in the British Isles.

Field work would be required to collect regurgitate samples at different colonies, involving capturing chicks at nests, but this is routinely done in several kittiwake colonies in the UK, Europe and US.

Information on timing of the chick-rearing period (i.e. date of first chick) is not routinely submitted to the SMP database but this information can easily be collected by experienced recorders.

A thorough evaluation of the potentials and limitations of morphological vs. molecular diet analyses would be required to determine whether genetic analyses are appropriate as an alternative, or complementary, technique.

Predicted resources required to deliver this RO
RO3.9a is a desk-based review, largely based on data that have already been collected and compiled as part of other projects.

LOW resource requirement (less than 6 months and less than £50K).

RO3.9b is a field study and will require ideally more than one field season to capture yearly variability in diet composition and breeding success.

HIGH resource requirement (minimum of two years, more than £200K).

RO3.9c is a desk-based study compiling data from RO3.9a-b and other existing sources.

MEDIUM resource requirement (less than one year, less than £100K).

RO3.10 Assessing the current and future condition of alternative fish prey populations: a desk-based study

Evidence need / Rationale for doing this RO

Building more realistic PVA models requires being able to predict the trajectory of kittiwake population size under predicted scenarios of climate change within the time period over which population size is modelled. Exploring how kittiwake demographic parameters relate to on-going and future changes in prey availability is thus needed to increase certainty in model predictions. While there has been a lot of research looking at how both climate change and fisheries may impact UK kittiwake demographic parameters through changes in sandeel abundance and availability (see e.g. review in Mitchell *et al.* 2020), uncertainty remains around how ongoing and future changes in the distribution and abundance of other prey types (e.g. sprat, herring) in the North, Celtic and Irish Seas may affect kittiwake populations. In particular, previous research has indicated some discrepancy in the relationship between kittiwake productivity and abiotic variables, such as SST and timing of stratification, between colonies (e.g. Carroll *et al.* 2015; Frederiksen *et al.* 2007), and it is unclear whether this lack of regional consistency could be explained by differences in the prey kittiwakes are feeding on (e.g. the drivers that were looked at may not be meaningful in the context of non-sandeel prey).

Given that sandeel populations are declining due to climate change, focussing management measures around one prey species (i.e. sandeels) might not be effective, especially if kittiwakes can exploit other prey resources. The EcoWatt2050 project (https://www.masts.ac.uk/research/ecowatt2050/), in partnership with the University of Aberdeen, has produced 7 by 7km distribution maps for 2050 of where increases vs. decreases in the overlap between predicted kittiwake foraging grounds and sandeel distribution may occur (see results in Sadykova *et al.* 2017). What will happen to kittiwake populations in areas where sandeels are no longer available? Will other prey become available that will support these kittiwake colonies or will these colonies decline to extinction?

RO3.9 above establishes the extent to which kittiwakes currently forage on prey other than sandeels. RO3.10 will follow on from this by improving understanding of availability of alternative prey species. With this RO, it is proposed to review the literature on population status and trends, drivers of population dynamics, current fishery levels and projected impacts of climate change for forage fish other than sandeels, and put this knowledge in the context of how kittiwakes use the marine environment in the UK, what we know they eat during the breeding season and their demography.

This RO would build on results from RO3.9 which would provide evidence for current prevalence of non-sandeel prey in kittiwake diet and how that influences demographic rates such as productivity.

Work already underway

This RO will make use of the various data-sets available below.

Current and historic data on fish distributions in the North-East Atlantic, including data from the herring assessment working group, is available through ICES.

There are also some models available that predict changes in fish distribution in European waters in response to warming seas (e.g. Montero-Serra *et al.* 2015). A critical assessment of the methods and results would be required to assess the quality of the predicted mapping outputs to inform RO3.10.

We have a relatively good understanding of where kittiwakes breeding in UK colonies forage thanks to the intensive GPS tracking work from the RSPB: UK-wide predicted breeding distributions (Wakefield *et al.* 2017) and SPA-level hotspot maps (Cleasby *et al.* 2018).

The Marine Ecosystems Research Programme (MERP) has constructed, and continues to populate, a comprehensive time- and spatially-explicit database of diets for ten seabird species (including kittiwakes) in the British Isles. Information was extracted for kittiwakes on 25 March 2020: diet data is available for 17 different colonies spanning from 1963 to 2015 (between one and 17 years of data per colony).

Work required
As a first step to approach this RO, it would be useful to review the kittiwake diet literature and identify the alternative food sources for kittiwakes, and how diet composition has varied over time (as per Wanless *et al.* 2018) and space. This could be informed by the outputs of RO3.9a or by extracting information from the MERP diet database. This preliminary search will be useful to delineate what species and regions are most relevant for this RO. Then, the relevant information for each species and region would be collated by conducting a systematic literature review on the current and forecasted distributions and trends, drivers of population dynamics and current fishing levels for those prey species and areas.

The outputs of the literature review could be summarised in the form of seasonal distribution maps of Clupeids, Gadidae and other alternative forage fish species, and overlap them with information where and when current fisheries occur, and where kittiwakes are known to forage.

This RO could also make use of the results of the EcoWatt2050 project and explore what predicted changes in kittiwake foraging distributions due to changes in prey distributions mean for the sustainability of kittiwake colonies.

Benefits / Key outcomes
This RO will provide information on the current and future status and condition of non-sandeel prey types, which will help anticipate likely demographic responses of kittiwakes to climate change and changes to fisheries management.

Information gathered from this RO will help re-interpret some of the relationships between kittiwake breeding success and abiotic variables (e.g. SST, timing of stratification) as proposed in RO3.8, in the context of alternative prey types. For example, large-scale studies e.g. Carroll *et al*. 2015 and Frederiksen *et al*. 2007 found very different relationships for different colonies. Could this partly be explained by differences in the prey the kittiwakes are feeding on and what do the drivers they looked at mean in the context of non-sandeel prey?

Undertaking ROs 3.8, 3.9 and 3.10 together would greatly improve our understanding of how prey determines kittiwake demographics and resilience to additional mortality, e.g. from OWF. These three ROs together provide valuable information on how kittiwake populations are likely to change in the near future and the role of prey and fisheries in driving those changes, in the context of climate change. This provides important wider context to assessing the impact of OW development on kittiwake populations; a population that is likely to decline due to an absence of prey will not tolerate additional mortality well whereas a population that is likely to continue to perform well due to suitable prey (sandeel or other species) being available will be more resilient to additional mortality.

Risks / Inter-dependencies
This is a desk-based study, largely based on data that have already been collected and compiled as part of other projects; thus, there are no foreseeable significant risks. This RO will benefit from the outputs of kittiwake diet literature review (as described in RO3.9a) for identifying the prey species of interest.

Predicted resources required to deliver this RO

LOW resource requirement (less than 6 months, less than £100K).

RO3.11 Quantifying the effects of fisheries management on kittiwake demography

Evidence need / Rationale for doing this RO
Kittiwake demographics, particularly productivity, are known to be correlated with prey availability. For example, for kittiwakes breeding in the Flamborough and Filey Coast SPA and feeding on the Dogger Bank, Carroll *et al*. (2017) found lower sea temperatures and lower fishing mortality were associated with greater sandeel biomass, which in turn, had a positive relationship with kittiwake productivity and adult survival. Similarly, Frederiksen *et al*. (2008) reported suppressed productivity for kittiwakes breeding on the Isle of May when the Wee Bankie sandeel fishery was operating.

One possible conservation measure for increasing kittiwake productivity is closure of sandeel fisheries within foraging range of kittiwake colonies (Furness *et al.* 2013). When considering efficacy of conservation measures, the ability to monitor the effectiveness of proposed measures is a key consideration. In other words, if management of sandeel fisheries was proposed as a conservation measure, it would be important to have a monitoring plan capable of quantifying demographic responses to changes in fishing effort.

This RO involves designing a monitoring plan that would maximise power to detect changes in demographic rates that could be attributed to changes in fisheries management. This would be followed by data collection prior to changes in fishing effort, which would provide a baseline against which to assess demographic response to management.

Work already underway
Frederiksen *et al*. (2004, 2008) and Carroll *et al*. (2017) have previously demonstrated a relationship between sandeel fisheries and kittiwake demographic rates but in all cases, additional environmental data were included as explanatory covariates, e.g. sea surface temperature. This previous work should be used to inform both experimental design and subsequent data analysis as part of this RO.

Work required
This work would be undertaken in two stages:

RO3.11a Experimental design
The aim of this sub RO would be to design the optimum data sampling protocol to maximise power to detect change in demographic rates due to changes in fisheries management. This needs to include considerations such as:

- Which demographic rates to measure and what information about these rates is needed, e.g. productivity data could include timing of breeding, number of nesting attempts, number of nests with >1 chick, number of chicks fledging per nest, *etc*.
- At how many colonies should demographic data be collected, e.g. which are optimal control colonies?

- How many years of baseline information would ideally be needed prior to changes in fisheries management?
- What covariates would need to be collected? This would include i. biological covariates (e.g. information on where adult kittiwakes from each colony are foraging during the breeding season, provisioning rates, prey species fed to chicks), ii. evironmental covariates (e.g. sea surface temperature, sea stratification metrics), iii. fishery covariates (e.g. timing and size of fishery landings, fishing effort)?

The experimental design should provide a detailed programme of data collection for each year prior to and during implementation of changes in fisheries management. The design should include recommendations for analysing data collected, including modelling approaches. It should also have an iterative component allowing feedback from the first years of data collection and analysis to inform subsequent years of data collection to ensure maximum power is obtained from data.

RO3.11b Data collection and analysis

This sub RO involves collecting data as prescribed in the experimental design (RO3.11a). Data collection should begin as soon as possible, to maximise data collected to inform baseline estimates of demographic parameters prior to changes to fisheries management. The more baseline data collected, the greater the power to quantify changes in demographic rates following changes to fisheries management, especially given rapidly changing environmental conditions due to climate change. As soon as sufficient data are available, data analysis and interpretation should be initiated as this will inform subsequent data collection. For example, other covariates may be identified as being important explanatory variables in models and additional data collection may be required. Initial model structure could be informed by approaches used by Carroll *et al*. (2017) and Frederiksen *et al*. (2004, 2008) but other approaches may be more suitable, e.g. Bayesian integrated modelling.

Benefits / Key outcomes

This RO would ensure maximum power is derived from demographic data collected as part of monitoring and demonstrating the efficacy of conservation measures. By collecting data prior to changes in fishery management, a high-quality baseline can be established against which to assess changes in demographic rates, thereby increasing the chances of being able to demonstrate effectiveness of conservation measures. Additionally, evidence arising from this RO will assist with both improving the quality of empirical data on demographic rates at colonies of interest that can be used to parameterise PVA models, as well as augmenting our understanding of what drives kittiwake population dynamics and to better anticipate how populations are likely to respond to predicted offshore wind farm mortality.

Risks / Inter-dependencies

Data collection and modelling approaches have already been developed and published previously, making risks to this RO relatively low. However, there is a risk that even with a robust experimental design and high-quality data analysis, no effect from fishery management is found on demographic rates. This could be due to adult kittiwakes not foraging in areas currently subject to fishing pressure, adults switching foraging locations or switching prey or other reasons that mean current fishing pressure is not supressing kittiwake demographic rates.

Another risk is that baseline data are collected but no changes to fisheries management occur. However, the baseline data will still be very valuable for generating more up to date demographic estimates and improving confidence in demographic estimates, which will assist with PVA parameterisation. Additionally, use of covariates to assist with explaining variation in demographic rates will advance our understanding of what determines kittiwake demographic rates and consequent population dynamics. In other words, the results from this RO will still be extremely valuable in better assessing population response to offshore wind farm impacts, even without changes to fisheries management.

This RO would best be delivered concurrent to RO3.8 which aims to explain broadscale patterns in population growth rates at multiple colonies around the UK. Information from these broad scale patterns would help identify optimal control colonies at which more detailed information could subsequently be collected.

Predicted resources required to deliver this RO
RO3.11a is a desk-based study to produce a robust experimental design.

LOW resource requirements (less than 6 months and less than £50K).

RO3.11b would require substantial data collection and analysis. This would need to be informed by the experimental design and so it is not possible to predict resources required but they are likely to be significant, especially if carried out for many years, as would be required to fully understand population response to changes in fisheries management.

LOW-MEDIUM annual resource requirements but required for **many years** (approx. £50-£100k per year including data collection and analysis but likely to require multiple years of work).

RO3.12 Predicting the demographic consequences of various potential measures to manage pressures on kittiwake populations

Evidence need / Rationale for doing this RO
As kittiwakes use both the marine and terrestrial environment, they can be exposed to a wide range of pressures. Quantifying the relative impact of every potential pressure, as well as their interaction, on their population dynamics, is a daunting task. A key knowledge gap is understanding how the removal or release from some of these pressures would enable population increase. This is relevant to offshore wind development as management of pressures has the potential to compensate for mortality from offshore wind development as well as making kittiwake populations more resilient to additional mortality. Whilst reducing one effect might not be enough to permit population increase, the interaction between pressures and demographic processes could mean population responses to reduced anthropogenic mortality could be non-linear. However, a complex model that is parameterised with too many covariates (for which there may be insufficient data) and that is trying to test every conceivable mechanistic hypothesis or combination of hypotheses bears the risk of not being viable (e.g. it is not possible to parameterise the model due to a lack of data), and, even producing spurious results. A more strategic and tractable approach would be to focus on the proximate causes of apparent population decline (i.e. too many birds die, not enough birds fledge, too many birds leave the colony) to help pinpoint the ultimate drivers of apparent decline (e.g. food availability, extreme weather), and then include only those pressures on kittiwake populations that can be managed. For example, while we cannot do anything about climate change directly, we can do something about nest site availability or commercial fisheries (see e.g. Furness *et al*. 2013 for a review of conservation measures).

Work already underway
Demographically structured state-space models can help apportion observed population variability to the proximate drivers of population change (i.e. age-specific mortality, productivity and population movements). This approach identifies which demographic parameter(s) are responsible for an observed decline in population size and then use covariates to try and determine which anthropogenic pressure(s) is/are likely to be influencing that demographic rate. This has been successfully carried out for populations of

marine mammals and seabirds (Caillat *et al.* 2019; Horswill *et al.* 2016a; Matthiopoulos *et al.* 2014; Miller *et al.* 2019). This approach allows the reconstruction of time-series for (often unobserved) demographic rates, which can then be expanded by the inclusion of environmental covariates (Caillat *et al.* 2019; Horswill *et al.* 2016a). In this way, we first find out for instance, that a population decline is due to 1st year mortality, we then obtain an error-corrected time series of that demographic rate and we finally regress that against covariates such as anthropogenic mortality. All three of these steps can be taken simultaneously in the same model to make sure that uncertainty is correctly propagated to the results.

Work required
The proposed modelling framework is structured as a two-stage process: 1) identifying the proximate causes of population decline, followed by 2) testing the effectiveness of a series of candidate management measures.

RO3.12a Identify the proximate causes of population decline

The first step of the modelling framework would be structured as follows:

- Develop an abstracted but realistic demographic model that captures density dependence and metapopulation processes, and accounts for both observation and process uncertainty, such as proposed under RO3.1;
- Test and refine the model by teasing out the effects of various demographic rates;
- Identify proximate causes of decline over time (i.e. the demographic rates that most strongly determine population size and growth rate);
- These different steps would then allow identifying candidate covariates (single pressures and combination of pressures) that can affect these demographic rates, and then those that can be managed. At this point, depending on availability of covariate data (e.g. variation in fishing effort or annual predation rates over time), it may be possible to quantify the contribution of specific pressures by including them as covariates of the most influential demographic parameters identified above. In case data on those specific pressures are not available at all, or not available in the right form to enable easy incorporation into the model, it would be valuable to direct future data collection on those ultimate causal mechanisms of population change to then be able to incorporate these covariate data in the model.

RO3.12b Quantify the relative contribution of candidate covariates on kittiwake population change

This sub-RO would involve incorporating covariate data into the existing model structure (as described in RO3.12a) to quantify their relative contribution in population change. Collection of additional covariate data may or may not be required, but in case it is required, this sub-RO would undertake that. Then, with covariate data in hand, it would be possible to test a series of management measures, by evaluating the population response that could be achieved through a plausible range of reduction in pressure(s) through management. The range of plausible values could be informed by previous research (e.g. effect size of the relationship between sandeel fishery closure and productivity/adult survival).

Benefits / Key outcomes
A similar state-space model structure is proposed to be developed under RO3.1. Therefore, by using a similar model structure, there is the potential for addressing two ROs simultaneously. This RO will differ from RO3.1 by adding additional complexity to the state-space model in the form of additional pressures on kittiwake populations.

This RO will provide key evidence to inform discussions around conservation management measures. It will assist with understanding the relative impact of offshore wind development on kittiwake populations, compared with other pressures.

Risks / Inter-dependencies
The proposed baseline modelling framework has already been developed and tested on kittiwake colonies in Shetland. Expertise also exists among academics in the UK, Europe and US to build, parameterise and interpret these complex models. Altogether, this means that risks are minimised around model development.

A major risk is around availability of covariate data, as they may not be readily available in a suitable form for testing the effectiveness of management measures. However, undertaking this RO in two sequential stages would allow first addressing some of the important questions related to proximate causes of decline and the potential pressures driving the decline. The model could then be expanded as and when covariate data become available.

Predicted resources required to deliver this RO
RO3.12a The first stage of the model can be developed without the need to collect new data and is based on existing code (similar model structure as the "Miller model").

MEDIUM resource requirements (less than one year, less than 100K)

RO3.12b Depending on the availability and format of the covariate data, there may be additional work required to sort these datasets or collect some new data, before being able to integrate this information into the existing model structure (RO3.12a) and test management measures.

LOW to MEDIUM resource requirements. This depends on whether additional effort is required to work on covariate datasets or collect new empirical data:

- If covariate data exist in a suitable format and only fitting the model with the covariate data is required: about 6 months and less than £50K;
- If covariate data already exist but work is required to re-format datasets: 6 months and less than £100K (in addition to the time and budget required for scenario A);
- If covariate data do not exist and additional work is needed to collect adequate covariate data: from 6 (spanning one breeding season) to +48 months (spanning two breeding seasons) or more (spanning multiple breeding seasons) and about £50-100K per year**.**

5 Synergies and overarching notes

The present report outlines a list of twelve research opportunities (ROs), which either alone or in combination with other project ideas, will improve our understanding of kittiwake population dynamics in the context of offshore wind development. These ROs are a combination of both large-scale strategic approaches and smaller-scale mechanistic approaches, involving both modelling or field work, with varying timescales and resource requirements.

RO3.1 is an important place to start as it provides an overarching framework for testing important hypotheses. RO3.1 will predict how likely kittiwakes are to move between colonies by modelling connectivity as a function of distances between colonies and the arrangement of the entire colony network. These estimates could then be refined by incorporating the results of ringing and relocation studies as proposed in RO3.3. Mark-recapture studies will inevitably take a few years to deliver useful information, but in the meantime, robust modelling approaches could be developed so that this information is analysed in the best way possible. Undertaking RO3.4 in parallel will quickly deliver useful information on population-specific adult survival rates, which could be incorporated to the different population models described under RO3.1, RO3.5, RO3.6 and RO3.12, and be complemented by the outputs of RO3.3. On the other hand, the outputs of RO3.1 will help identify the most influential population parameters for reconstructing time-series and reducing the uncertainty around population trajectories, and hence will inform RO3.3 as for where and how monitoring effort should be targeted. Another direct application of RO3.1 is to allow new functionality to be added to existing PVA modelling approaches (RO3.2) and hence increase biological realism.

Food availability is an important driver of kittiwake population dynamics, and better understanding of what affects food availability during the breeding season and how kittiwakes are able to adapt to these changes is crucial to assess resilience of populations in the context of climate change and fisheries pressures, and identify potential mitigation measures to improve population viability. In this respect, desk-based studies that review the available information on kittiwake diet patterns (RO3.9), current and future prey distribution and status of prey (RO3.10) and examine ecosystem processes driving the relationship between productivity and proxies of climate change (RO3.8) will provide a solid knowledge base to direct future collection of empirical evidence and test hypotheses including the effectiveness of conservation measures (as in RO3.12). Meanwhile, a desk-based study that develops a robust experimental protocol for quantifying the effects of fisheries on kittiwake demography (RO3.11) will inform the effectiveness of possible conservation measures.

6 Conclusions

This report has set out a series of twelve potential research opportunities (ROs) which were suggested and discussed during and subsequent to a workshop of experts in kittiwake population dynamics. Most of the projects described consist of more than one stand-alone piece of work, for example RO3.3 and RO3.9 include a desk-based study and a field element. Although they have been brought together into coherent ‘projects’, an element of ‘pick and mix’ is possible, for example if limited budgets do not allow for each full project idea to be pursued as a whole. Equally, some of these projects represent exploratory or feasibility assessments, and depending on the outcomes of these, could pave the way for much larger data-collection projects, and this has been pointed out and described briefly where appropriate. Furthermore, there are synergies and efficiencies within and across KGs, e.g. RO3.3 is very similar to RO2.3 in KG2, with both ROs exploring the use of mark-re-sighting systems to improve understanding of connectivity between SPAs and OWF as well as between colonies (immigration/emigration). Thus, undertaking one RO may well deliver key evidence to greatly assist with another RO.

The intention is that this report provides a signpost towards research which can contribute to reducing uncertainty around the linkage of effects on kittiwakes seen at a wind farm to populations, and thus contribute to overall reduced uncertainty in offshore wind farm environmental impact assessments. Incremental reductions in uncertainty will become more important as the offshore wind sector expands, in order to facilitate meaningful and precise cumulative impact assessments, therefore maximising the potential for sustainable marine development within the limits set by environmental protection and regulation.

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