Document Number
WO1-WOW-PER-ENV-RPT-0032

Revision 01

Approved

Mr Stuart McAuley - Offshore Wind Power Limited

Oct 2, 2024, 5:10 PM GMT+1:00

West of Orkney Windfarm

Offshore Ornithology Technical Supporting Study 12

Annex 1P:
Seabirds and highly pathogenic avian influenza

Date:	09 May 2023
Tel:	0141 342 5404
Web:	www.macarthurgreen.com
Address:	93 South Woodside Road |Glasgow | G20 6NT

Document Quality Record

Version	Status	Person Responsible	Date
0.1	Draft	Prof. Robert W. Furness	10/10/2022
0.2	Reviewed	Dr Ross McGregor	13/10/2022
0.3	Updated	Prof. Robert W. Furness	23/11/2022
1	Internal Approval	Dr Ross McGregor	25/11/2022
1.2	Updated	Dr Nicola Goodship	02/05/2023
2	Internal Approval	Dr Ross McGregor	09/05/2023

MacArthur Green is helping to combat the climate crisis through working within a carbon negative business model. Read more at www.macarthurgreen.com.

CO_2e Assessed Organisation

CONTENTS

LIST OF TABLES

LIST OF FIGURES

EXECUTIVE SUMMARY

Birds (wild and domestic) have long been exposed to low pathogenicity avian influenza (LPAI) which causes little or no illness in affected birds. However, highly pathogenic avian influenza virus (HPAIV) is a mutated strain of avian influenza that evolved in domestic poultry in Asia and kills a high proportion of infected birds. Originally confined to domestic birds in high-density poultry farming, this infection eventually escaped into wild birds and has spread around the world.

HPAIV hit great skuas at several colonies in summer 2021 and then hit great skuas again, even harder in 2022 when it also hit gannets, terns and guillemots, and to a smaller extent several other seabird species at colonies around the UK and throughout the North Atlantic. These HPAIV outbreaks were unprecedented in North Atlantic seabirds. It is very difficult to assess how many birds died, but it is likely that about 50% of adult great skuas died and perhaps 25% of adult gannets. Impact may have been large on common guillemot and on some tern colonies (especially Sandwich terns in The Netherlands and east England) but it is even more difficult to quantify in those species. However, there is a high risk that further outbreaks will occur in seabirds in the 2023 breeding season and in subsequent years. Some surviving seabirds are likely to develop resistance to HPAIV but depletion of populations may be considerable.

Ecological theory and empirical evidence suggest that seabird populations are likely to recover from depletion by HPAIV as a consequence of compensatory density-dependence. Although theory predicts the possibility of ecological or genetic Allee effects/depensatory density-dependence affecting seabird populations that are reduced to very small numbers, empirical evidence for Allee effects (depensatory density-dependence) is very limited and in many cases appears to be overwhelmed by influences of average nest site quality increasing as colony size declines (a compensatory density-dependent relationship). There is little or no evidence that genetic Allee effects occur in seabird populations reduced to very small size, and there is no clear evidence for any strong Allee effects in most seabird species (desertion of colonies by terns subject to predation impacts may represent a significant depensatory effect in those species but may also be seen as birds moving to higher quality nest sites where breeding success can be higher).

Recovery of seabird populations depleted by HPAIV may take many years and possibly several decades. Populations might never recover to previous numbers if carrying capacity has reduced as a consequence of ecological change (climate change in particular, but also change in fisheries management affecting availability of food to scavenging seabirds). It is likely that many seabird breeding features of Special Protection Areas (SPAs) in Scotland will be considered to have moved from favourable conservation status to unfavourable conservation status as a consequence of depletion of breeding numbers by HPAIV. It seems unlikely that this anthropogenic strain of avian influenza could be considered a normal environmental pressure for seabirds since it is as anthropogenic as seabird bycatch or plastic pollution.

It will be important to take account of the effects of the HPAIV epidemic on seabirds in the West Orkney Windfarm (the Project) impact assessments. Key to any impact assessment is matching the time scales of the site-based data collection used to inform the impact assessment with the colony based counts used in the assessment. The majority of the digital aerial survey data collected for the proposed development were obtained prior to the severe population level effects on seabirds. Adjusting the analyses of data on a species by species basis could be used to prevent incorrect

comparisons of impact levels with mismatched population size estimates. Population size estimates could be adjusted based on current, precautionary, knowledge of the impacts of HPAIV infection on adult populations, but these should only be used with predicted impacts on demographic rates, not absolute predicted impacts from the proposed development. Guidance from stakeholders will need to be taken into account as it emerges.

1 INTRODUCTION

1. Highly Pathogenic Avian Influenza virus (HPAIV) hit seabirds around the North Atlantic in 2022, causing mass mortality of breeding adult great skuas *Stercorarius skua*, Sandwich terns *Thalasseus sandvicensis* and gannets *Morus bassanus*, and killing smaller numbers of gulls, Arctic terns *Sterna paradisaea* and common terns *S. hirundo*, auks, and fulmars *Fulmarus glacialis*. This outbreak was unexpected and largely caught seabird ecologists by surprise, although there had been a much smaller outbreak in great skuas in 2021. The impact of HPAIV on seabirds will only become clear in a few years from now, which causes problems for the assessment of impacts of offshore wind farms on seabirds. Not only may baseline conditions be altered by mortality caused by HPAIV, but behaviour of seabirds may alter as a consequence of HPAIV, and the population dynamics of seabirds may change as a consequence of changes in density-dependence resulting from acute mortality reducing seabird population size. This report considers these issues based on the limited information available about HPAIV in seabirds and the more extensive literature on density-dependence in seabirds and case studies on seabirds subject to severe and acute depletion of population size.

2. Virus testing in dead wild birds is carried out by the Animal and Plant Health Agency (APHA) which is an executive agency of Defra and also works on behalf of the Scottish Government and Welsh Government. Defra has a hotline for communication of mass mortality of wild birds. However, existing policy is only to test one or two individuals of each affected species from each region every few weeks, and so the vast majority of seabirds that died from HPAIV were not tested for the virus. Numbers testing positive for HPAIV listed by Defra provide very little indication of the scale or location of HPAIV outbreaks. For example, 1,500 dead adult great skuas at Foula in summer 2022 were initially considered not to need testing because several great skuas elsewhere in Shetland had already tested positive for HPAIV. Eventually Defra/APHA agreed to test a maximum of three birds from Foula, all of which tested positive for the virus. In contrast, several gannets washed up on beaches were tested in many counties around the UK but provide little or no indication of where most of that mortality occurred; more gannets from beaches in Cornwall were tested than from beaches in Shetland, despite very much higher numbers of gannets being affected by HPAIV in Shetland than in SW England.

3. SNCBs communicate closely with APHA about virus testing, but the huge numbers of seabirds found dead in 2022 all around the UK presented a major challenge to resource available for virus testing. NatureScot provided fortnightly summaries of HPAIV in Scottish seabirds through 2022, but that list, although very helpful and informative, was indicative rather than comprehensive. There is no comprehensive database of HPAIV impacts on wild birds.

4. Although risk to humans from HPAIV is very small, globally there have been hundreds of human deaths caused by contracting Avian Influenza, almost all associated with poultry farming, with a very high death rate for those who contract the infection from infected birds (WHO 2022). Therefore, UK and Scottish Government guidance is for people to avoid contact with dead birds that might carry HPAIV. This is a sensible precaution but has inhibited research into the outbreaks in 2021 and 2022 in UK seabird populations.

5. Four forms of HPAIV transmission from infected birds to healthy birds should be considered: (1) as a result of the consumption of infected prey or carrion by predators or scavengers, (2) by transfer of virus in secretions or in the air, most likely between adjacent birds in colonies but potentially in flocks elsewhere, (3) through faeces excreted by infected birds, and (4) from virus shed into freshwater from infected birds or leaching from carcasses of dead birds (Camphuysen et al. 2022). Although close physical contact between individual birds at colonies is most likely to promote infection, influenza viruses deposited into the environment by wild birds may also lead to further infections and mortality events (Ramey et al. 2022). Water-borne HPAIV transmissions were the main determinants of disease dynamics and observed prevalence levels in the Camargue (France), which highlights the importance of the persistence of viral particles in water to infect wild birds (Roche et al. 2009). Fresh-water bodies, or wetlands, may represent an important medium in which infectious influenza viruses reside outside of a biotic reservoir. There is little information regarding the persistence of infectious influenza viruses in the field at ambient temperatures, but in a study in one of the mildest climate zones in Alaska, some influenza A viruses remained viable for more than one year (Ramey et al. 2022). However, the relative importance of these different means of transmission remains unknown, and almost certainly varies considerably according to the ecology of each seabird species. It might be reasonable to guess that scavengers such as great skuas and large gulls would be likely to pick up infections from feeding on seabirds that have died from HPAIV, while transmission between birds at colonies might be most important where birds nest in close physical contact (as with terns, common guillemots *Uria aalge*, kittiwakes *Rissa tridactyla*) but be less likely with seabirds that nest far apart (as with skuas) or in burrows (as with puffins *Fratercula arctica*, shearwaters, storm-petrels).

6. Natural England produced guidance in September 2022 on HPAIV in seabirds and offshore wind farm impact assessments in English waters (NE 2022). They state "We are currently unclear what the short, medium and long-term effects of the 2022 HPAI outbreak will be on seabird colony abundance and vital rates (productivity and survival). We expect HPAI to remain a threat to UK breeding seabirds for the foreseeable future. It will take several years for data to be gathered on abundance, mortality and productivity, so we will need to work with imperfect knowledge in the interim. We must work collectively to ensure that seabird populations are made more resilient to the type of catastrophic event caused by HPAI. This includes delivering the actions relating to feeding, breeding and survival as outlined in Natural England's recommendations to Defra in the England Seabird Conservation and Recovery Plan". While these points relate specifically to England, the guidance will be broadly relevant to considerations in Scotland. Similar guidance is likely to be produced by NatureScot and Marine Scotland.

7. We may learn more about HPAIV in seabirds over the next few months. It is likely that some scientific papers will be published and there are plans for various Workshops. For example, NatureScot plans a workshop on 27 October. BTO plans a workshop on 2 November and two more later in November. This report must therefore be seen as interim in a situation where new information may well appear soon.

2 HPAIV IN SEABIRDS IN NW EUROPE IN 2021 AND 2022

2.1 A need for caution in interpreting "facts"

8. Published scientific papers mostly avoid erroneous facts and unsubstantiated claims as a result of the rigorous peer-review process. However, with the HPAIV epidemic arising suddenly and before most scientists could engage in the study of impacts on seabirds, there are very few peer-reviewed published accounts. Where much of the evidence is available only from web pages, tweets, blogs, and newspaper articles, it is necessary to be very cautious about facts being presented. Even apparently reputable organisations may appear to provide highly misleading information.

9. For example, according to BirdLife International's statement on HPAIV in seabirds in 2022 (posted 8 August 2022) "more than 80% of the UK's great skua population have been affected a country home to roughly 90% of its global breeding population", "The Netherlands lost up to 80% of its breeding population of Sandwich terns in a couple of weeks", and "over 20,000 dead northern gannets being washed ashore in Canada" (BirdLife 2022). No references are cited to support any of these facts.

10. The first 'fact' is simply wrong. RSPB estimate that 56% of the global population of great skuas breeds in the UK (RSPB 2022). The global breeding population of the great skua was estimated at 16,000 pairs by Mitchell et al. (2004) with 60% of these in the UK, far below the 90% stated by BirdLife. According to BirdLife, the global population of the great skua is 16,300 to 17,200 pairs (BirdLife datazone[1]), similar to the estimate by Mitchell *et al*. (2004). Breeding numbers in the UK have increased in some smaller colonies since 2000 but have decreased considerably at some of the largest colonies (Furness 2022; JNCC 2022). Numbers in some regions overseas such as Norway and Russia have increased considerably, so the estimate that 90% of the global population is in the UK is incorrect now, as it was in the recent past. The BirdLife estimate that 80% of the UK's great skua population has been affected by HPAI in 2022 also appears to be a guess and probably an exaggeration. The most detailed study at any great skua colony in 2022 was by Camphuysen and Gear (2022) at Foula. They reported a 57% decline in breeding numbers at Foula in 2022 compared to the previous census in 2015, with the reduction by the end of the 2022 breeding season estimated at between 60 and 70%. Not only is their estimate well below the BirdLife 80%, but this colony was already declining in numbers (Furness 2022), so HPAIV is unlikely to be the only cause of decline since 2015. Most great skua colonies in the UK were not investigated at all in 2022, so the scale of the loss in most colonies is simply unknown yet. It seems unlikely that more than 80% of the UK great skua population died in 2022, but no accurate figure can be given yet.

11. The second 'fact' is not entirely consistent with reported detailed studies on Sandwich terns in The Netherlands in 2022. That research found 8,001 dead adults at ten colonies (22% of breeding adults) plus another 1,600 dead adults away from colonies (Rijks et al. 2022, Mardik Leopold pers. comm.) from a population estimated at 30,000 to 40,000 breeding adults (Rijks et al. 2022). However, the researchers concluded that most of the remaining adults were likely to have become immune to HPAIV, that at an eleventh colony there was no mass mortality and a 'normal' fledging success, and that about 600 pairs that had abandoned an

---

[1] http://datazone.birdlife.org/home

infected colony bred at a new nearby site with very little sign of any HPAIV mortality (Rijks et al. 2022, Mardik Leopold pers. comm.).

12. The third 'fact', that over 20,000 gannets were washed ashore in Canada seems not to be supported by any authoritative published evidence. Professor Bill Montevecchi, the leading expert on gannets in Canada has suggested that many thousands of gannets died, but that the impact of HPAIV on seabirds in Canada in 2022 was more severe for guillemots than for gannets, and that it is unlikely that 20,000 gannets were counted on Canadian coastlines. When I emailed BirdLife to ask where the estimate of over 20,000 gannets being washed ashore in Canada came from, they said they could not find any such source but that 20,000 was 10% of the population estimate, and they simply changed the online post to '*over 8,000 dead northern gannets being washed ashore in Canada*'. The '*over 8,000*' "fact" appears to be based on suggestions by Radio Canada that about 8,000 seabirds, mostly gannets, were washed up on Canadian beaches (Radio Canada 2022). However, Professor Montevecchi suggested that guillemots died in larger numbers than gannets, so even the 8,000 total may not be taken as an accurate estimate of gannet mortality. Radio Canada noted that whereas large numbers of gannets died in the Magdalen Islands and Acadian Peninsula, very few were affected by HPAIV at Bonaventure Island. In relation to Bonaventure Island, they quote seabird ecologists as saying "*we are talking about a few hundred dead gannets in a colony of more than 100,000 individuals. There is almost no difference visually*". Indeed, breeding numbers at Bonaventure Island were considered to be higher in 2022 than in 2020 (Radio Canada 2022). Clearly HPAIV did have a big impact on gannets in Canada, but the scale of the mortality seems rather uncertain, and apparently highly variable among colonies.

13. A National Geographic article titled "The UK's largest avian flu outbreak has left millions of birds dead – and scientists extremely concerned" (National Geographic 2022) quotes an RSPB spokesperson "*We haven't seen a species go globally extinct in Europe since the last two great auks were hunted down off the coast of Iceland in 1844. Seabird populations are already extremely poor in heart, so for some like the great skua, bird flu could be the straw that breaks the camel's back: we cannot let the species go extinct on our watch*". No source for the estimate of "millions of birds dead" is provided, but "millions" apparently refers to numbers of chickens culled at chicken farms to prevent further spread of the disease in intensive poultry farming, so does not relate to impacts on wild birds, despite the expressed concern about great skua extinction risk. The great skua might be at risk of extinction from HPAIV, but the evidence available so far does not give strong grounds to expect that outcome.

14. These examples simply serve to indicate that extreme care needs to be taken when evaluating evidence about HPAIV impacts on seabirds presented online, in social media or newspaper articles. We have tried to be careful in this report to avoid presenting any misleading or unsupported data by:

    1. Carefully evaluating the original reports that present estimated impacts;
    2. Not repeating any reported impacts that are themselves unsupported by a cited data source;
    3. Presenting citation details of the original reports so that these can be followed up for further detail;
    4. Where reports lack details of the methods used or the original source, we have tried to contact the authors to obtain these details, or we have contacted local seabird

ecologists with good knowledge of the populations/colonies to get their expert opinion;

5. We have cited named expert opinion as in litt or pers comm to indicate exact sources of evidence.

15. Nevertheless, we emphasise that all estimates of impacts of HPAIV on seabirds in 2021 and 2022 outlined in this report must be treated with great caution, because of the difficulty of obtaining accurate measures under the extremely challenging circumstances of an unprecedented epidemic.

2.2 The origin of the HPAIV epidemic in seabirds

16. Avian influenza has been affecting wild and domestic birds for many decades. Many wild birds have resistance to the low pathogenicity strains of avian influenza (LPAIV) and show only mild symptoms if any, when infected. The evolution of a "new" strain of avian influenza, H5N1, or so-called HPAIV, has changed the situation dramatically. The H5N1 lineage of the avian influenza virus arose in the early 1990s and became endemic in poultry (originally in domestic geese) in southeast Asia (Chen *et al.* 2005). It has circulated in chicken farms since the early 1990s, resulting in mass culls of chickens when outbreaks occur. A H5N1 outbreak affecting wild geese was reported in 2005, and this was the first reported instance of a highly pathogenic strain of avian influenza causing mass mortality in wild birds. In Europe, further outbreaks have occurred annually in wild birds, especially waterfowl, since 2006 (Globig *et al.* 2009, Cui *et al.* 2022), while Asian-origin HPAIV infections in wild and domestic birds in the New World were detected for the first time in winter 2014/15 (Jhung and Nelson 2015). In virtually all earlier outbreaks, migratory Anseriformes (mostly wild geese and ducks) and Charadriiformes (waders and some gulls) were involved, and mortality issues were most prominent in winter. Breeding seabirds were seemingly unaffected, or mass mortality events could not be attributed to HPAIV outbreaks, even though certain seabird species, notably auks, also acted as hosts of low pathogenic influenza virus variants (Huang *et al.* 2014, Wille *et al.* 2014, Lang *et al.* 2016). Over three decades, the ecology of HPAIV H5N1 has significantly changed from sporadic outbreaks in domestic poultry to persistent circulation in wild birds (Sonnberg *et al.* 2013). Migratory birds have played a role in moving the virus around the world, and this can be traced from phylogenetic analysis of virus genome. For example, a clade found in poultry in South Korea in January 2014 was rapidly carried by migratory waterfowl around much of the northern hemisphere (Lycett *et al.* 2016). Over the years, infections have been detected in an increasingly wide range of bird species including wildfowl, waders, gulls, terns, cranes, grebes, herons, pelicans, gamebirds, corvids, raptors, but also more recently in mammals, including humans (Kaplan and Webby 2013, Huang *et al.* 2014, Wille *et al.* 2014, Lang *et al.* 2016, Convention on Migratory Species 2022, WHO 2022).

17. In 2018, HPAIV was detected in swift terns *Thalasseus bergii* and several other seabird species on the west coast of South Africa. In 2021, more than 24,000 Cape cormorants *Phalacrocorax capensis* and Cape gannets *Morus capensis* died on the west coast of South Africa and in 2022 the virus was detected in the endangered African penguin *Spheniscus demersus* near Cape Town (Daily Maverick 2022).

18. Some 2,500 pelicans died of HPAI in late January 2021 in Senegal/Mauritania (BirdLife 2022). However, the first major outbreak of HPAIV in breeding seabirds in Europe was not detected until late summer 2021.

2.3 The HPAIV outbreak in North Atlantic seabirds in 2021

19. Exceptional mortality of breeding adult great skuas was reported in July 2021 on several Scottish islands, prompting a disease investigation which subsequently detected HPAIV H5N1 clade 2.3.4.4b as the cause of the mortalities (Banyard *et al.* 2022). The first dead great skuas were reported just before the end of June, HPAIV infections were confirmed on 20 July, and the last casualties were found in autumn 2021. Affected areas were Hirta (St Kilda), the Flannan Isles, Orkney, and seven locations in Shetland (Fair Isle, Mainland, Papa Stour, Noss, Yell, Fetlar, Unst). H5N1 infections were detected in samples taken at St Kilda, the Flannans and Fair Isle. At St. Kilda (with a population of at least 211 Apparently Occupied Territories (AOTs) in 2019; JNCC 2022) and Fair Isle (430 AOTs in 2020; JNCC 2022), more than 10% of the breeding birds were found dead, with the very likely possibility that more birds had died but were not found (Banyard *et al.* 2022). Breeding productivity at the colonies was very low in 2021, possibly as a consequence of the HPAIV outbreak. One great black-backed gull *Larus marinus* that died at the Flannan Islands also tested positive for HPAIV but only in bulk viscera and not in swab material (Banyard *et al.* 2022). The HPAIV outbreak in 2021 in great skuas has apparently been overlooked by some ornithologists who suggest that the 2022 outbreak was the first to occur in UK breeding seabirds (e.g. Pearce-Higgins and Toms 2022).

20. At Foula, Shetland, in 2021 unusually high mortality of adult great skuas was noticed with at least four times as many dead adults as normal early in the breeding season and several sick adults seen later in the season (Gear 2022). Breeding success in 2021 was zero in the monitoring area, the first time complete breeding failure by great skuas had ever been recorded at Foula (Gear 2022), but no dead birds from Foula were tested for HPAIV. Given the similarity of events at Foula in 2021 to the cases at other great skua colonies nearby, it seems reasonable to assume that HPAIV affected the birds at Foula too.

21. No unusual mortality of any other seabirds was noticed at colonies in Scotland in 2021, suggesting that the epidemic of HPAIV was limited to great skuas. However, Camphuysen and Gear (2022) note that in April 2021, seven times the normal background densities of dead gannets were recorded on beaches in The Netherlands, the highest number in the 45 years of data (**Figure 1**). When great skuas travelled towards their breeding grounds in April 2021, they must have encountered unusual numbers of dead gannets floating within the southern North Sea. If those gannets had already been infected with HPAIV (causing the unusual mortality rates in April 2021), this could explain how great skuas (as scavengers) have picked up the virus on their way to their own colonies in spring 2021. In spring 2022, great skuas were seen scavenging on dead gannets at sea, and the even higher peak in numbers of dead gannets in the southern North Sea in spring 2022 (**Figure 1**) suggests that this same pattern most likely occurred in both these years. Apparently almost all these dead gannets were in full adult plumage and were in very good body condition with plenty of subcutaneous fat (Kees Camphuysen, pers. comm.), indicating that they had not starved as is often the case with beached birds. This strongly hints at HPAIV killing gannets in spring in the southern North Sea in 2021, but unfortunately none of those dead birds were tested for the virus.

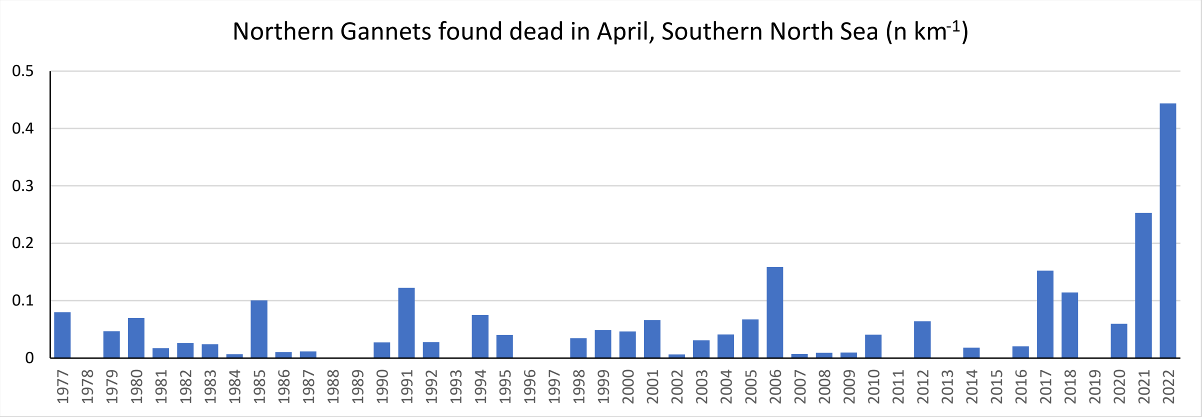

Figure 1. Long-term beached-birds survey data of northern gannets in April in the southern North Sea, based on systematic surveys in The Netherlands (Camphuysen and Gear 2022, calculated from data published in Camphuysen 2022).

2.4 The HPAIV outbreak in North Atlantic seabirds in 2022

22. HPAIV was confirmed in eider ducks *Somateria mollissima* at Shetland and a great black-backed gull at Fair Isle in April 2022 (Philip and Tyler 2022). The first clear indication of the resumption of the epidemic of HPAIV in North Atlantic seabirds in 2022 was detected in mid-April 2022, when unprecedented numbers of dead adult great skuas were found at Foula, Hermaness, Fetlar, Noss, and Fair Isle. At about the same time, dead great skuas were again being found at St Kilda. Very soon it became clear that northern gannets were also being affected, with dead gannets at the colonies at Hermaness and Noss and in the sea around Shetland. At Shetland in May or June a small number of other seabird species tested positive for HPAIV, including herring gull *Larus argentatus*, great black-backed gull and Arctic tern, but up until the end of June almost all mortality attributed to HPAIV was in great skuas and gannets. Shetland great skua colonies were thought to have declined in breeding numbers attending colonies by more than 50% by late June, but it is impossible to know how much of the decline was due to birds leaving the area because of the situation rather than dying of HPAIV. It is likely that some partners of birds that died may have abandoned the area and some pairs may have chosen to do so. Reduced numbers at colonies cannot be assumed to indicate the scale of mortality, just as it would be inaccurate to assume that numbers of dead birds found at colonies indicate the total numbers that died from HPAIV. It appeared that immature/nonbreeding birds abandoned colonies exceptionally early, presumably in response to the sudden mortality event occurring. Miles *et al*. (2022) report that over 1,000 gannet corpses were seen at Hermaness and over 1,000 gannet corpses were seen at Noss, the vast majority being full adults. Gannet AONs at Noss in 2022 at 11,472 AONs were 17% lower than the count in 2019, but it is uncertain whether the "missing" birds had died or abandoned the colony because of the situation in 2022. Only 103 great skua AOTs were found on Noss in 2022, down by 78% from the 476 AOTs in 2018. On Mousa, great skua AOTs in 2022 (36) were 40% down from the most recent count (60 AOTs in 2017). By the end of the summer positive HPAIV tests had been obtained from dead birds sampled in Shetland of eider, great skua, gannet, Arctic tern, herring gull, great black-backed gull, and long-tailed skua *Stercorarius longicaudus*. A few dead seabirds were seen (as normal or slightly more than normal) for Arctic tern, kittiwake and large gulls. However, only great skua, gannet and eider were

observed in exceptional numbers of dead birds at Shetland. There was no sign of HPAIV affecting any auks or petrels in Shetland. Despite HPAIV in great skuas and gannets, Arctic tern and kittiwake had an unusually good breeding season in Shetland in 2022 with increased numbers and increased breeding success compared with recent years, while guillemot and razorbill did at least as well as in recent previous years (Miles *et al*. 2022).

23. HPAIV was not noticed in seabird colonies in Orkney until mid-May, when it was confirmed in great skuas in Orkney. In June, very small numbers (mostly fewer than 5 individuals) of great black-backed gulls, kittiwakes, common guillemots, common gulls *Larus canus* and fulmars were affected at Orkney.

24. In the Western Isles, great skuas were found dead in large numbers at colonies at St Kilda, Lewis, Barra and Mingulay and in small numbers on beaches throughout the Western Isles. Gannets were affected at St Kilda and were also washed up on beaches throughout the Western Isles. Almost all individuals on beaches were in full adult plumage despite there being immature birds flying past the area (Bob Furness, pers. obs.). There were no signs of HPAIV affecting seabirds at Canna, Colonsay, Staffa or Mull in May-June 2022, although that changed later in the season.

25. In east Scotland, there were higher than normal numbers of dead gannets on beaches from May onwards. Sandwich terns at St John's Pool, Caithness were affected, but Sandwich terns at Sands of Forvie were not (Philip and Tyler 2022). Small numbers of great black-backed gulls and herring gulls were affected, but the main mortality was in gannets at Troup Head and Bass Rock (Philip and Tyler 2022). Although a few adult great black-backed gulls were dead on the shore at East Caithness Cliffs SPA in May and June, breeding numbers at the main colonies in the SPA were slightly higher in 2022 than they had been in 2021 or 2015 (Bob Furness, pers. obs.) suggesting that HPAIV had not significantly affected overall breeding numbers of that species in East Caithness Cliffs SPA. Large numbers of common guillemots, razorbills *Alca torda* and puffins were affected at St Abb's Head, and HPAIV was detected in seabirds at the Isle of May, but the impact there was apparently smaller than at St Abbs Head (Philip and Tyler 2022).

26. Relatively late in the seabird breeding season, over 150 adult common terns were found dead on the Avoch tern raft (Moray Firth) and HPAIV is thought to have killed half the population there (Philip and Tyler 2022). Over 50 kittiwakes were very freshly dead in mid-July at a colony of about 150 pairs at Berriedale, East Caithness Cliffs SPA (Bob Furness, pers. obs.) where at the same time large numbers of chicks were just fledging. Large numbers of dead guillemots were found on beaches in east and west Scotland in August-September 2022, suggesting that significant mortality of auks probably occurred late in the breeding season. Over 1,000 dead guillemots were reported from the west coast of Scotland (Philip and Tyler 2022). Quantifying that impact is unlikely to be possible at present since birds were dispersing away from colonies at the time so the evidence for the impact will probably not be available until birds return to colonies in spring 2023. However, Highland Ringing Group received over 100 recoveries of dead ringed adult guillemots from the Canna colony in late summer-early autumn, most of those being found on the coast of Skye (Bob Swann, pers. comm.), which is an unprecedented number of recoveries of ringed adult auks from that colony within a single autumn.

27. Presence of HPAIV was tested in samples of dead seabirds by APHA on behalf of Defra. Only small numbers were tested, and only from sites that were convenient for sampling (for example only three great skuas from Foula were tested from the 1,500 dead adults found there, but all three tested positive for HPAIV). Seabirds testing positive in Scotland in summer 2022 included great skua (Shetland, Orkney, Handa, St Kilda, Lewis), gannet (Shetland, Orkney, Western Isles, east and west coasts of mainland Scotland), common guillemot (east and west coasts of mainland Scotland), razorbill (Golspie and Islay), puffin (Isle of May, St Kilda, Islay), Arctic tern (Shetland, Isle of May), Sandwich tern (Caithness), great black-backed gull (Shetland, Handa), lesser black-backed gull *Larus fuscus* (Handa), herring gull (Caithness, east coast of mainland Scotland), common gull (east coast of mainland Scotland), black-headed gull *Chroicocephalus ridibundus* (Aberdeenshire), kittiwake (Caithness, Isle of May), Manx shearwater *Puffinus* (Rum). In addition, great northern diver *Gavia immer* (Embo) and eider (Shetland and Isle of May) tested positive. The overall picture is that great skua and gannet were very severely affected at most of their colonies in Scotland, while many other species of seabirds in Scotland were affected in small numbers at some colonies but the impacts on the other species were of very uncertain magnitude and highly variable among locations. In late September a fulmar sampled from north Scotland tested positive for HPAIV, confirming the virus in this species which had appeared to be unaffected throughout spring and early summer. The extent to which fulmars became infected is uncertain as only relatively few were reported dead in late summer, but this indicates that the infection may well have spread into some other seabird species without being evident. There is uncertainty as to whether any storm-petrels have been infected, and the infection of Manx shearwaters (which was confirmed at Rum) appears to have been minimal but has not been assessed in detail (Philip and Tyler 2022).

28. In east England, HPAIV infection arrived at the Farne Islands SPA, where over 4,000 dead seabirds were collected for disposal (National Trust web pages and Gwen Potter, pers. com.). These included guillemots, kittiwakes, razorbills and terns. At Coquet Island SPA, the 2022 seabird breeding season appeared at first to be very promising with increased numbers of Sandwich terns (2,214 pairs) and roseate terns (154 pairs) in particular. Small numbers of dead adults were found from 19 May to 16 June, with one or two each day (Alfarwi 2022). However, large numbers of birds, predominantly terns, died between 17 June and 31 July, with 2,122 dead birds (this total including chicks as well as adults) collected and buried (in an attempt to reduce spread of the virus). According to Natural England about 50% of adult roseate terns at Coquet Island SPA died of HPAIV in 2022 (NE 2022). According to Alfarwi (2022) about 54% of roseate tern nests were “lost” with deaths of 60% of the chicks, while 100% of the Sandwich tern chicks died. At Coquet Island a great skua that was present through the summer and scavenged on dead terns and gulls also died. It was suggested that the mobility of tern chicks was highly likely to have caused the rapid increase in deaths of terns in late June (Alfarwi 2022) but it is unclear whether human disturbance at the colony (including walking through the tern colonies collecting dead birds each day) may have increased the movement of infected chicks and so contributed to the spread of the infection.

29. There was mortality of seabirds at Flamborough and Filey Coast SPA and of Sandwich terns, in particular at North Norfolk Coast SPA. According to Natural England about 10% of Sandwich tern adults at North Norfolk Coast SPA died of HPAIV in 2022 (NE 2022). Gannets at

Grassholm, at colonies in Ireland and at colonies in the Channel Islands were also affected, but relatively late in the summer compared with colonies in the north.

30. Elsewhere in the North Atlantic HPAIV was confirmed in seabirds from The Netherlands to Spitsbergen, Iceland and Canada. Great skuas and gannets were particularly severely affected at most or almost all of their North Atlantic colonies, including in the Faeroes, Iceland, Canada and Bear Island. Hundreds of adult gannets died at Helgoland, Germany, and as at some UK gannet colonies, breeding success there was exceptionally low at around 0.1 chicks per nest (Volker Dierschke, in litt.). Sandwich terns were severely affected in The Netherlands (Rijks et al. 2022), but HPAIV also occurred in gulls and other terns there (Kees Camphuysen pers. comm.).

31. Virus sequence phylogenetic analysis showed that HPAIV was transported by migratory birds, probably geese, from Europe to Newfoundland (Caliendo et al. 2022a). In Canada, some tens of thousands of seabirds died, with the outbreak starting in May 2022 in gannets south-west of Newfoundland, then spreading east to colonies off the south and east coasts of Newfoundland in July, and then northwards into Labrador in August (Bill Montevecchi, in litt.). In Canada, the highest mortality was thought to occur in guillemots, with somewhat lower mortality in gannets and razorbills and less still in puffins, kittiwakes and gulls and some apparently very limited mortality of fulmars and shearwaters (Bill Montevecchi, in litt.).

32. The outbreak in great skuas and gannets at Foula was monitored in great detail by Kees Camphuysen and Sheila Gear who carried out daily searches over different parts of the entire island to build up a map of the locations of dead great skuas and to investigate the ecology of the disease in this colony. They found 1,500 dead adult great skuas at the colony. Their report represents the most detailed study carried out on HPAIV in a seabird colony (Camphuysen and Gear 2022). Based on the condition of corpses, the deaths began in mid-late April, but most died during late May. Early in the epidemic the deaths mostly occurred at or close to freshwater bathing sites, but with relatively more of the late deaths occurring within nesting territories. Birds died very suddenly, in good body condition, and usually with spasms that resulted in freshly dead birds being in characteristic posture (shown in numerous photos in that report). Camphuysen and Gear (2022) noted a 57% decline in breeding numbers (AOTs) of Great Skuas at Foula in comparison with census results obtained in 2015. They concluded that, given ongoing mortality throughout the summer, this must be seen as a conservative estimate and that a 60-70% decline in occupied territories is likely.

33. It is likely that a clearer picture of the impact of HPAIV on Scottish seabird populations will emerge in 2023 or later years, when changes in the numbers in breeding colonies will become apparent. However, it is highly likely that at least half of the breeding adult great skuas in Scotland died from HPAIV in the outbreaks in 2021 and 2022. Numbers of dead gannets at St Kilda, Hermaness, Troup Head and Bass Rock were in the low thousands at each of these sites, but whereas great skuas seem mostly to have died at colonies, many gannets died at sea and some washed up on coastlines throughout Europe. That makes estimating numbers that died almost impossible at the present time. It is likely that at least 10% and possibly more than 30% of breeding adult gannets from Scottish colonies may have died from HPAIV in 2021 and 2022 (mostly in 2022). Impacts on breeding numbers of guillemots may have been substantial at some colonies in 2022. Impacts on other seabird species appear to have been smaller and more localised. However, it seems highly likely that there will be further

outbreaks in the 2023 breeding season (and possibly on the wintering grounds of some seabirds), so the medium-term impacts of HPAIV on seabirds may be considerably worse than what occurred in 2022 alone. Furthermore, with major impacts on the same seabird species in other countries too, there will be little scope for recolonisation by immature birds from overseas coming to Scottish colonies to fill gaps created by HPAIV.

3 RESPONSES OF SEABIRDS TO ACUTE IMPACTS TO POPULATIONS

3.1 Theoretical predictions

34. Ecological theory predicts that as colonies of seabirds increase in breeding numbers there will start to be increased competition for limiting resources leading to density-dependent reductions in mean fitness of individuals, resulting in reduced population growth. This is known as compensatory density-dependence, or negative density-dependence, and is widespread throughout nature. For colonial seabirds, limiting resources might be food around the colony or high quality nest sites, but the outcome is the same. As population size grows density-dependence will reduce breeding success, increase age of first breeding, reduce survival, or increase net emigration or a combination of these. Where seabird populations are close to environmental carrying capacity, an acute impact that reduces numbers moderately will reduce density-dependent competition, leading to improved demography that will tend to restore numbers towards carrying capacity. The population will naturally "bounce back" from the acute impact to restore numbers.

35. However, if numbers are reduced to very low levels then theory predicts the possibility of positive density-dependence, more often called an Allee effect, named after an American ecologist who developed the theory in this regard. Positive density-dependence reduces individual fitness as population size or population density decreases. Allee effects can be categorized as "strong" or "weak". Weak Allee effects reduce growth rate when population size is very small but growth rate remains positive so that population increases, though more slowly at first until numbers build up somewhat. Strong Allee effects occur if the growth rate falls negative when population size falls below a critical threshold abundance. If strong Allee effects occur, a population that is reduced below critical threshold numbers will decline at an increasingly rapid rate to local extinction.

36. Allee effects can be ecological or genetic. Ecological effects can occur if, for example, predation rates increase as bird numbers decline. This is likely in colonial species if adult birds communally defend eggs and chicks such that defence is less successful when numbers are smaller. Similarly, if foraging is communal/social then reduced numbers may reduce average foraging success. Ecological Allee effects can also include problems for individuals to locate a mate when population density is much reduced, but this is unlikely to be an issue for colonial seabirds as most immature birds can spend several years looking for a suitable colony to recruit into, and most start this process by returning to the colony where they were born. In some animals there is a need to modify the habitat, and that may be difficult when population size is very small, but this also is unlikely to apply to colonial seabirds.

37. Genetic effects can arise as a consequence of small population size leading to inbreeding, loss of genetic diversity (the genetic bottleneck effect) or genetic drift. Inbreeding increases when a population has become very small, so that fitness is reduced by inbreeding depression caused by increased phenotypic expression of deleterious recessive genes. A genetic bottleneck effect and genetic drift are also processes that become prominent specifically when population size is extremely small.

3.2 Empirical evidence relating to negative density-dependence (compensation) in seabird demography

3.2.1 Observational/correlational evidence

38. Horswill *et al.* (2017) reviewed published evidence for compensatory density-dependence in seabirds. Compensatory density-dependence was found across all of the demographic processes and seabird taxonomic groups that they reviewed with a variety of causal mechanisms. Across 89 studies of 27 species, significant evidence of compensatory density-dependence was found in 67 of the studies. These authors concluded that there is widespread evidence of the importance of compensatory density-dependence in seabird populations. Mechanisms of compensatory density-dependence included a relationship between recruitment into individual colonies and the availability of high quality nest sites, density-dependent relationships between availability of limiting resources and age of first breeding, rate of recruitment from the pool of nonbreeders, or in the incidence of nonbreeding. Numerous studies reported compensatory density-dependence in relation to population growth rate, adult survival, juvenile survival, breeding success and dispersal and the balance between immigration and emigration. In many cases the most obvious density-dependent compensation related to numbers of available nest sites (which is relatively easily quantified) but relationships were also evident with food supply around the colony (which is often more difficult to quantify). However, mechanisms of compensatory density-dependence also included examples of increased disease transmission at higher population density (Pöysä and Pöysä 2002), decrease in clutch size at higher population density (Coulson 1999), increased conspecific disturbance at higher population density (Grear *et al.* 2009) and increased cannibalism of chicks at higher population density (Coulson *et al.* 1982).

39. Horswill *et al.* (2017) fitted a relationship between seabird population size and population growth rate to illustrate the form of density-dependence. They used data for six types of seabird, including a diver, a scoter, a gannet, and three species of gull (kittiwake, herring gull and Audouin's gull *Ichthyaetus audouinii*). This showed a significant relationship, with population growth rate highest for the smallest population size and declining with increase in population size. However, that plot assumes that one individual of any of the included species is equivalent to one individual of any of the other species (despite a gannet weighing about six times as much as a kittiwake) and assumes that the carrying capacity baseline remains constant through the data time series. Because seabirds are long-lived but their prey is short-lived and subject to fluctuations driven by the environment, carrying capacity may fluctuate considerably. That may in part explain why the plot showed very high variance of population growth rate, especially close to the intercept (Horswill *et al.* 2016). The plot can be taken as further evidence for the importance of compensatory density-dependence, but with limited value in identifying the specific form of that relationship. Since the review by Horswill *et al.* (2017) several further studies have reported further examples that indicate clear evidence of compensatory density-dependence.

40. Modal age of first breeding by great skuas at Foula, Shetland, was seven years old in the 1970s when numbers were increasing and breeding success was high. However, age of first breeding increased at this colony in the 2010s when population size was declining due to reduced carrying capacity. By comparison, age of first breeding was younger at smaller

colonies (Handa, Fair Isle) indicating compensatory density-dependence in this demographic parameter (Furness 2015).

41. Juvenile survival of Audouin's gull decreased strongly with population size, indicating strong compensatory density-dependence (Payo-Payo *et al*. 2016).

42. Time-series analysis of herring gull and lesser black-backed gull population sizes in the British Isles showed compensatory density-dependence in the herring gull, and lesser black-backed gull showed faster population growth at lower herring gull densities (Nager and O'Hanlon 2016).

43. A positive association between availability of fishery discards and open-air refuse disposal on the egg volume of yellow-legged gulls at 20 colonies in the western Mediterranean was mediated by compensatory density-dependent mechanisms which was interpreted as relating to a density-dependent increase in competition for food for breeding birds (Real *et al*. 2017).

44. Analysis of tracking data for four species of breeding seabirds (kittiwake, common guillemot, razorbill and shag *Gulosus aristotelis*) in British and Irish waters showed that distribution at sea is dependent on compensatory density-dependent competition among sympatric conspecifics and in the case of kittiwake and common guillemot also on competition with conspecifics from neighbouring colonies (Wakefield *et al*. 2017), as originally inferred by Furness and Birkhead (1984) from the spatial distribution of different sizes of colonies.

45. Lamb *et al*. (2017) found evidence for compensatory density-dependent effects on foraging by breeding brown pelicans *Pelecanus occidentalis* with foraging range from the colony increasing with colony size. Individuals from larger colonies were more likely to migrate and travelled longer distances than individuals from smaller colonies. These authors concluded that "*density-dependent competition may be an important driver of both the extent of foraging ranges and the degree of migration exhibited by brown pelicans*".

46. A 49-year study of a wandering albatross *Diomedea exulans* population found that population size explained 60% of the variation in juvenile survival as a consequence of compensatory density-dependence, but that climate change had a stronger effect on overall population dynamics (Fay *et al*. 2017).

47. Analysing time series data for five seabird species in Alaska showed that all five populations exhibited compensatory density-dependent effects on population growth, but that the carrying capacity of the environment had changed considerably, increasing for common guillemots and Brunnich's guillemots *Uria lomvia*, decreasing for black-legged kittiwakes and tufted puffins *Fratercula cirrhata*, but remaining relatively stable for red-legged kittiwake *Rissa brevirostris* (Goyert *et al*. 2017). Subsequent analysis identified climate change as responsible for these changes in carrying capacity (Goyert *et al*. 2018).

48. Analysis of Humbolt penguin *Spheniscus humboldti* chick body condition at different sized colonies showed compensatory density-dependence, with evidence for local prey depletion around colonies (Cortes-Hinojosa *et al*. 2017).

49. Despite potentially confounding effects of industrial fisheries depleting forage fish off Peru, state-space models demonstrated strong evidence of compensatory density-dependence in

the abundance of the three key seabird species of the Peruvian upwelling ecosystem (Barbraud *et al.* 2018).

50. An integrated population model of Audouin's gull based on a 28-year data set found that productivity and immature survival were the main drivers of population change, being high when the population was small but showing strong compensatory density-dependence (Genovart *et al.* 2018).

51. South polar skuas *Stercorarius maccormicki* showed reduced population growth as the population size increased, as predicted with compensatory density-dependence. This study inferred that competition for food and nesting space both are likely to be causal mechanisms for this pattern (Pacoureau *et al.* 2019).

52. Population modelling of kittiwakes validated against empirical time series data showed that models lacking compensatory density-dependence fail to provide realistic results, as do models that assume populations are closed to immigration/emigration. Realistic population models for seabirds require incorporation of density-dependence and meta-population structure (Miller *et al.* 2019).

53. Analysis of demographic parameters of kittiwakes over a 20-year period of change in colony size indicated that apparent survival of immature birds was strongly influenced by colony size during a cohort's second year, indicating compensatory density-dependence of immature survival, or colony-fidelity, in this population (McKnight *et al.* 2019).

54. Analysis of foraging trips by breeding Adelie penguins *Pygoscelis adeliae* showed that intra-specific competition for food around the colony was a major compensatory density-dependent influence on this species (Kokubun *et al.* 2021). Studying the same species, Southwell *et al.* (2021) provide evidence from analysis of population growth rates at colonies of Adelie penguin over 70 years that compensatory density-dependent effects have reduced the growth rate of the meta-population and individual colonies in East Antarctica, probably through a combination of limiting nesting habitat and limiting prey availability close to colony sites. The same authors previously concluded that suitable breeding habitat may be more limiting than food in this population, but that conclusions about food-limitation were hampered by lack of data on food availability (Southwell and Emmerson 2020).

55. In great cormorant *Phalacrocorax carbo*, chick body condition was negatively correlated with estimated foraging density of cormorants around the colony, especially within a range of 20 km. It was concluded that the size of the colony itself and of the nearest neighbouring colonies and the associated variation in density of foraging cormorants were major drivers of variation in chick condition between colonies and between years (Bregnballe and Frederiksen 2021).

56. The food-constraint mechanism for compensatory density-dependence at seabird colonies (often referred to as Ashmole's halo based on his theoretical prediction of the effect) was demonstrated empirically at a large seabird colony by Weber *et al.* (2021) by quantifying seabird foraging density and prey fish abundance around a major seabird colony. Prey fish abundance increased with distance from the colony up to a distance of >150 km.

57. Common guillemots at the Isle of May disproportionately used higher quality nest sites when sub-colony size was smaller, resulting in higher breeding success at lower population size (compensatory density-dependence), but new sites were established under all situations and

those new sites could be of lower quality, which could act to slow population recovery after periods of reduced colony size (Bennett *et al*. 2022).

58. Tracking data were used to show that chick-rearing season foraging ranges of guillemots increase with colony size scaled to power 0.33, consistent with the theoretical expectation resulting from compensatory density-dependent depletion of prey resources around colonies (Patterson *et al*. 2022).

59. Changes in the numbers of great skuas in colonies in Scotland from 2000 to 2020 showed that small colonies grew considerably whereas the largest colonies either declined or increased only very slightly in numbers (**Figure 2**). Numbers of great black-backed gulls in colonies in Scotland all decreased from 2000 to 2020, but decreases were much larger at larger colonies (**Figure 3**). For both species, these changes were interpreted as being the result of compensatory density-dependence with a decrease in carrying capacity in recent years in terms of food availability (Furness 2022).

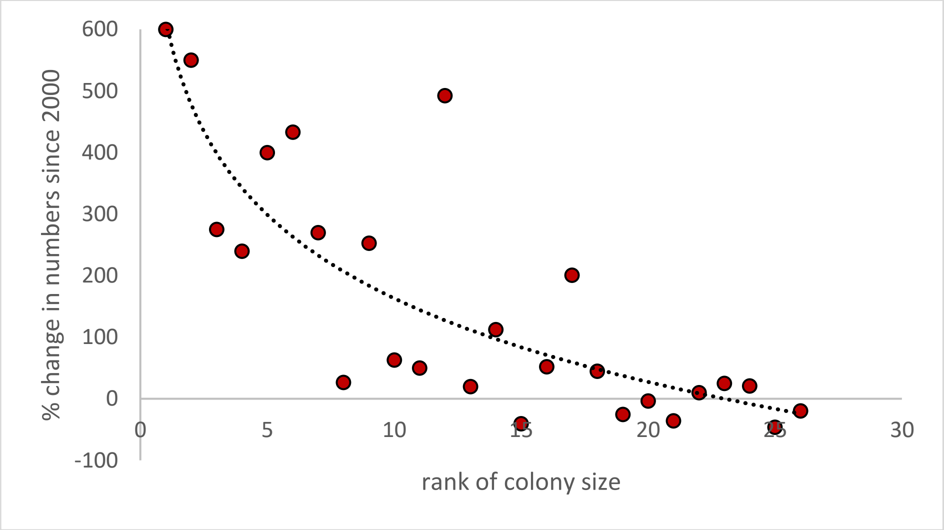

Figure 2. Change in breeding numbers of Great Skuas at colonies in Scotland since Seabird 2000 (up to 2020) in relation to rank of colony size (from smallest rank 1 to largest rank 26). The dotted line shows the best fit logarithmic regression (r=-0.825, p<0.001). From Furness (2022).

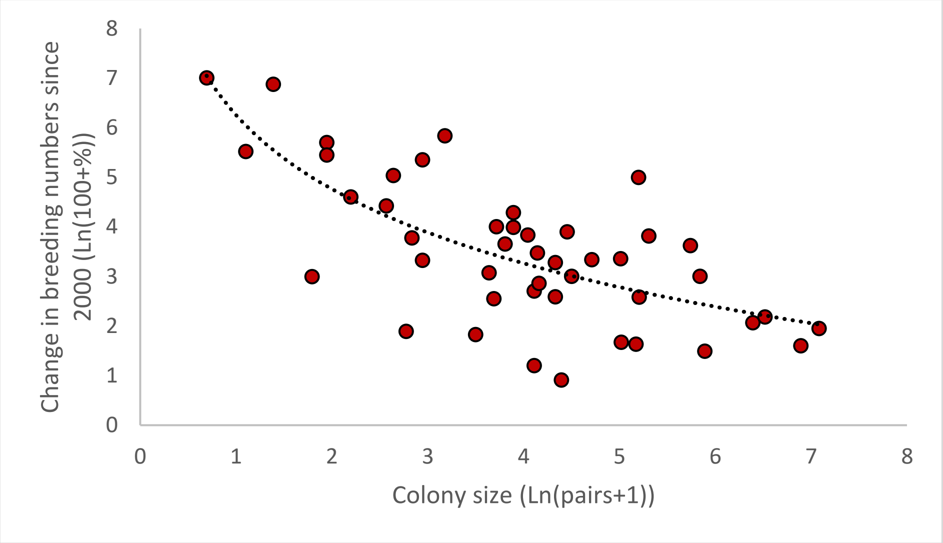

Figure 3. Change in breeding numbers of Great Black-backed Gulls (Ln transformed) at colonies in Scotland since Seabird 2000 (up to 2020) in relation to colony size (Ln transformed). The dotted line shows the best fit logarithmic regression (r=-0.708, p<0.001). From Furness (2022).

60. All of the above, taken together, provides overwhelming evidence for the importance of compensatory density-dependence in seabird populations, such that small to moderate reductions below environmental carrying capacity will result in changes to various demographic parameters that increase population growth rate to tend to bring numbers back towards carrying capacity.

3.2.2 Experimental evidence: culling

61. In addition to the observational/correlational evidence reviewed in 3.2.1, there is experimental evidence of compensatory density-dependence in seabird populations. Experimental evidence is often considered to be stronger than observational evidence because experimental design can avoid some of the potentially confounding relationships that might exist in purely observational studies. Culling of very large numbers of gulls at certain colonies provides a strong example of the response of a seabird population to experimentally-reduced population density.

62. At the Isle of May, Firth of Forth, the Nature Conservancy Council (NCC) culled about 45,000 herring gulls between 1972 and 1981. This reduced the colony size from an estimated 15,000 pairs in 1972 to about 3,700 pairs (Coulson *et al.* 1982). Several aspects of herring gull demography altered as a consequence of this cull. Firstly, the age of first breeding became younger. Before the cull there were no records of 3rd year birds breeding but after the cull some birds started to breed when only 3 years old, and the mean age of first breeding reduced by over one year (Coulson *et al.* 1982). There was evidence that the proportion of young birds returning to recruit into the Isle of May colony increased. Body weight and wing length of breeding herring gulls increased as the population size was reduced. There is evidence that this increase took place within individual cohorts and that individual birds gained body condition as a consequence of reduced competition either in the breeding or

feeding areas (Coulson *et al*. 1982). Younger herring gulls lay smaller eggs than older herring gulls. However, despite the effect of culling being to reduce the average age of breeding gulls in the colony, average egg size increased, which also was considered to reflect an improvement in the body condition of adults as a consequence of reduced competition. All of these changes were interpreted by Coulson *et al*. (1982) as strong evidence of compensatory density-dependence that would result in the impact of the cull being mitigated.

3.3 Empirical evidence relating to positive density-dependence (depensation) in seabird demography

63. Gascoigne and Lipcius (2004) presented theoretical work confirming that Allee effects can be driven by predation. Since predation is a widespread phenomenon, this suggests that Allee effects could be widespread in nature. However, they noted that there are few empirical data confirming the existence of Allee effects. Gascoigne and Lipcius (2004) concluded that conservation biologists should be aware of the possibility of Allee effects in very small populations where extinction is likely, but that empirical evidence for these effects being important is very limited. Modelling indicates that Allee effects might be responsible for reduced recolonization distances when tern colonies are extirpated by predation, leading to parts of metapopulations becoming more isolated (Schippers *et al*. 2011). This may make Allee effects less detectable in populations that have high rates of immigration/emigration between colonies.

64. In their literature review of density-dependence in seabirds, Horswill *et al*. (2017) found 11 out of 89 studies identified examples of depensatory (i.e. positive) density-dependence compared with 67 that reported compensatory density-dependence. Depensatory density-dependence was almost completely limited to increased predation of eggs and chicks at lower population densities, and was mostly observed in terns, small gulls and auks. The causal mechanism for depensatory predation was attributed primarily to the spacing of adults influencing the ability of a predator to approach nests, and to a limited extent to decrease in breeding synchrony and incubation tenacity at lower nesting densities (Horswill *et al*. 2016).

65. Yellow-legged gulls *Larus michahellis* are predators on Audouin's gull eggs and chicks. Analysis of the relationship between Audouin's gull breeding success and the relative abundances of Audouin's gull and yellow-legged gull in the area showed evidence of negative and positive density-dependence in this association (Oro *et al*. 2006). Breeding success decreased where Audouin's gulls were at high density, indicating negative density-dependence. Breeding success also decreased where the local abundance of yellow-legged gulls exceeded the local abundance of Audouin's gull, indicating predatory depensatory density-dependence (Oro *et al*. 2006). However, in this case study, depensatory density-dependence only became evident when the absolute abundance of the predator exceeded the abundance of the prey species, which is a relatively rare situation in ecology.

66. Apparent survival of adult Mediterranean gulls *Ichthyaetus melanocephalus* at colonies of different size in Belgium and The Netherlands showed no change across small colony sizes, but apparent survival of juveniles increased from colonies of <100 pairs to about 600 pairs (te Marvelde *et al*. 2009). This indicates no depensatory density-dependent effect for adult survival (or dispersal) but an effect for juvenile survival (or dispersal). For both adults and

juveniles, apparent survival decreased with colony size when colonies were of more than 600 pairs, indicating negative density dependence across larger colony sizes. Highest survival in juveniles approximately coincided with the average colony size. For juveniles the depensatory effect was small (survival increasing from 0.5 in the smallest colonies to 0.6 at 600 pairs, and considerably smaller than the compensatory effect (juvenile survival falling from 0.6 at 600 pairs to <0.3 at 1,300 pairs.

67. Minias *et al.* (2015) found that fledging success of common terns was 30% higher on a raft holding *ca.* 100 nests than on three rafts holding 30-40 nests each but that chick body condition was poorer on the raft with larger number of nests. They cross-fostered chicks between the large and small rafts and showed that differences in chick condition were not inherited but were determined by local environmental conditions (specifically higher intraspecific competition at the raft with larger number of nests). Evidence for depensation in terms of fledging success may therefore possibly be confounded by impacts on chick condition or the levels of stress in adults, although in this case it seems likely that a 30% difference in fledging success is likely to have a greater demographic effect than a difference in body condition of surviving chicks. Similarly, Phillips *et al.* (1998) found that Arctic skua *Stercorarius parasiticus* hatching success and post-fledging survival were higher in parts of the colony where nest density was higher because adults nesting close together were better able to mob and repel attacking great skuas. However, Arctic skua chick growth rate was lower in these high-density areas (Phillips *et al.* 1998). Although this example is one of the 11 cited by Horswill *et al.* (2016) as an example of depensatory density-dependence, that may not be the case if predation rates by great skuas are low. Under such conditions reduced chick growth may mean that density-dependence is compensatory, whereas under conditions of high predation rates the lower success of predation at higher nest density may be depensatory.

68. For species with positive density-dependence, costs and benefits of increasing density may depend on environmental conditions. Guillemots breeding at the Isle of May experienced a period of severe food shortage in 2007 and 2008 resulting in the lowest breeding success at this colony recorded over a 25-year period (Ashbrook *et al.* 2010). Birds were observed at nest sites to compare departures and arrivals of parents, food delivery to chicks, instances of aggression to chicks and any fatalities of chicks between low density and high density subgroups within the same colony under these adverse conditions. Birds at high density increased foraging effort more than birds at low density, often leaving their chick without a parent attending, whereas at low density unattended chicks tended to be killed by gulls or razorbills. However, at high density increased aggression of neighbouring conspecifics towards unattended chicks resulted in chick deaths, undermining benefits from collective defence against predators. The study concluded that there were previously unsuspected trade-offs between costs and benefits of increasing nesting density under changing environmental conditions (Ashbrook *et al.* 2010).

69. Predation rates by gulls on guillemot eggs and chicks were higher at declining colonies of guillemots because gulls were able to approach guillemot nest sites more easily when the birds nested at lower density (Gilchrist 1999). However, one consequence of decline in breeding numbers of guillemots was a shift to nesting in more protected sites. The birds studied by Gilchrist (1999) moved into areas inaccessible to gulls so avoided predation impacts when the numbers of guillemots reduced. Similarly, at Teuri Island, Hokkaido,

guillemot numbers declined from 40,000 birds in 1938 to 8,000 in 1963, and to just 19 in 2010 (Hasebe *et al*. 2012). Up until 1994 the guillemots almost all nested in open habitat on sea stacks and ledges. As the population declined the impact of predation of eggs and chicks by gulls increased. After 1994 the reduced numbers of guillemots only nested in caves where they were no longer exposed to nest predation and there has been no significant decline in numbers between 1994 and 2010 (Hasebe *et al*. 2012). In the caves, nesting success was higher, reducing the rate of population decline to a negligible level compared to the situation before 1994. Although theory predicts that predation can impose depensatory density-dependent mortality, this can be avoided where birds are able to select higher quality nest sites that are safe from predators, as in this case for guillemots at Teuri Island. Despite the population being reduced to just 18 birds in 1994 and remaining at about that number until 2010, the high nest site quality of the few remaining pairs allowed relatively high breeding success without risk of nest predation and therefore prevented detection of any Allee effect in that extremely reduced population.

70. Votier *et al*. (2009) found a weak but statistically significant relationship between guillemot population size and timing of breeding. When population size was 4,000 the median laying date was Julian day 137. When population size was 16,000 the median laying date was Julian day 132. Laying earlier tends to result in higher breeding success so this relationship could possibly be an Allee effect through, for example, social stimulation. However, Votier *et al*. (2009) warned that due to the correlative nature of this result considerable caution should be expressed in the interpretation of this.

71. In Shetland the local sandeel stock collapsed in the 1980s. Kittiwake breeding numbers at Shetland fell from 54,664 pairs in 1981 to 15,825 pairs in 2000 (Pennington *et al*. 2004). The decline was attributed not only to food shortage for breeding kittiwakes but also to predation by great skuas (Heubeck *et al*. 1997, Oro and Furness 2002). As numbers declined, an increasing proportion of the remaining kittiwakes nested in very sheltered situations such as the back of large caves or under overhangs where great skuas find it difficult to manoeuvre (Pennington *et al*. 2004). Breeding success was higher at sheltered colonies, higher where local numbers of great skuas were smaller, and the rate of decline of kittiwakes at Shetland colonies was much higher at exposed colonies than at colonies sheltered from great skuas (Votier *et al*. 2008). Kittiwake numbers declined at Foula from 4,350 AONs in 1987 to 259 AONs in 2019 before a slight recovery to 425 AONs in 2021. However, the decline is a loss of >94% of the population between 1987 and the minimum count in 2019. Nevertheless, a plot of $\log_{10}$ kittiwake AONs against year (**Figure 4**) shows no sign of any detectable Allee effect at this colony, despite it being adjacent to the largest great skua colony in the world and subject to heavy predation by great skuas (Oro and Furness 2002, Church *et al*. 2018). The rate of decline (the slope in **Figure 4**) remains consistent throughout, with no acceleration towards extinction as predicted if there was a weak Allee effect and no sudden drop to extinction as predicted if there was a strong Allee effect.

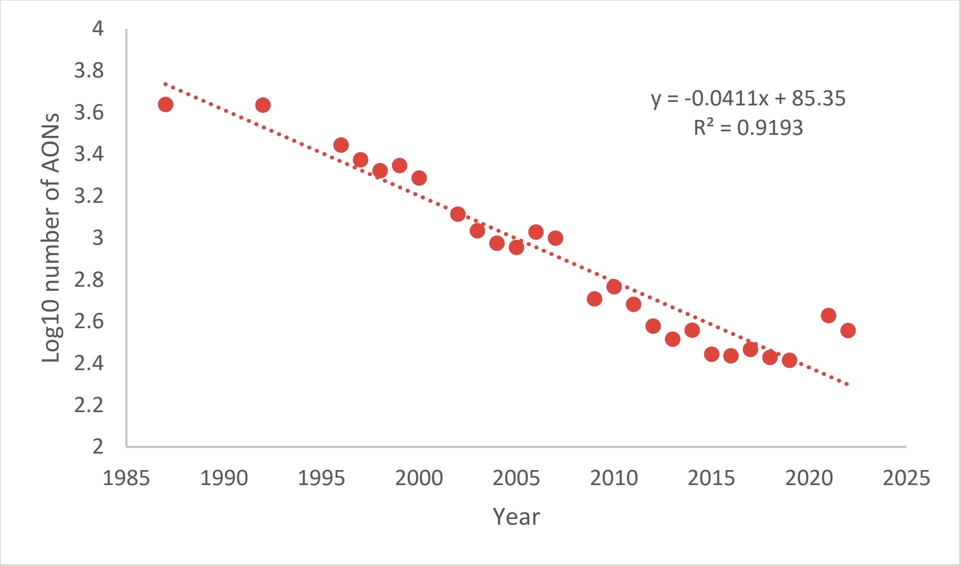

Figure 4. Log$_{10}$ of kittiwake AONs at Foula 1987-2022. Census data from JNCC Seabird Monitoring Programme online database with data for 2022 from Miles et al. 2022.

72. Kittiwake numbers declined at Fair Isle from 18,159 AONs in 1992 to 323 AONs in 2021. The decline is a loss of >98% of the population between 1992 and 2021. Nevertheless, a plot of log$_{10}$ kittiwake AONs against year (**Figure 5**) shows no sign of any detectable Allee effect at this colony, despite it being adjacent to a large great skua colony and subject to heavy predation by great skuas (Fair Isle Bird Observatory Annual Reports). The rate of decline (the slope in **Figure 5**) remains consistent throughout, with no acceleration towards extinction as predicted if there was a weak Allee effect and no sudden drop to extinction as predicted if there was a strong Allee effect.

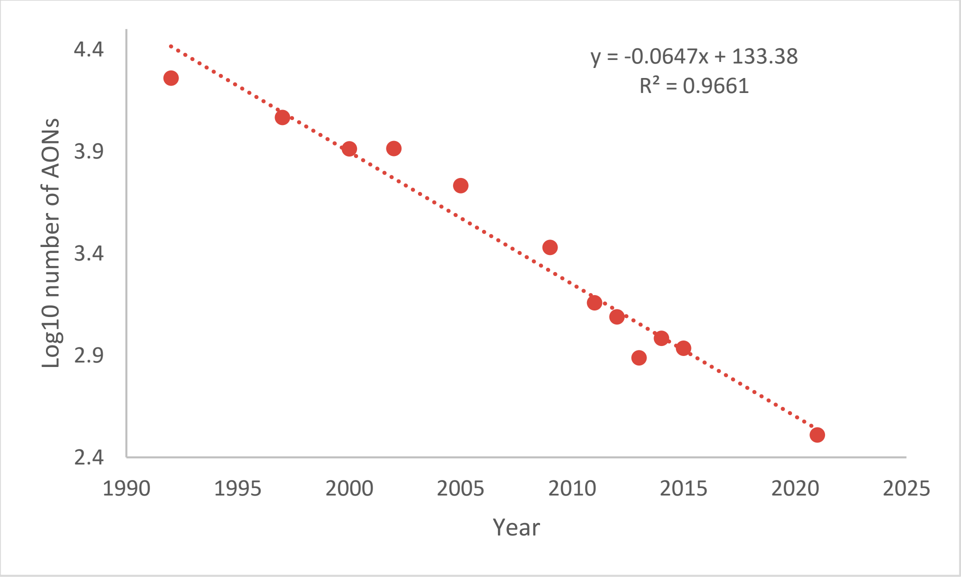

Figure 5. Log$_{10}$ of kittiwake AONs at Fair Isle 1992-2021. Census data from JNCC Seabird Monitoring Programme online database.

73. Kittiwake numbers declined at Noss from 9,438 AONs in 1985 to 44 AONs in 2017. The decline is a loss of >99.5% of the population between 1985 and 2017. Nevertheless, a plot of log$_{10}$ kittiwake AONs against year (**Figure 6**) shows no sign of any detectable Allee effect at this

colony, despite it being adjacent to a large great skua colony and subject to heavy predation by great skuas (Shetland Bird Reports). The rate of decline (the slope in **Figure 6**) remains consistent throughout, with no acceleration towards extinction as predicted if there was a weak Allee effect and no sudden drop to extinction as predicted if there was a strong Allee effect.

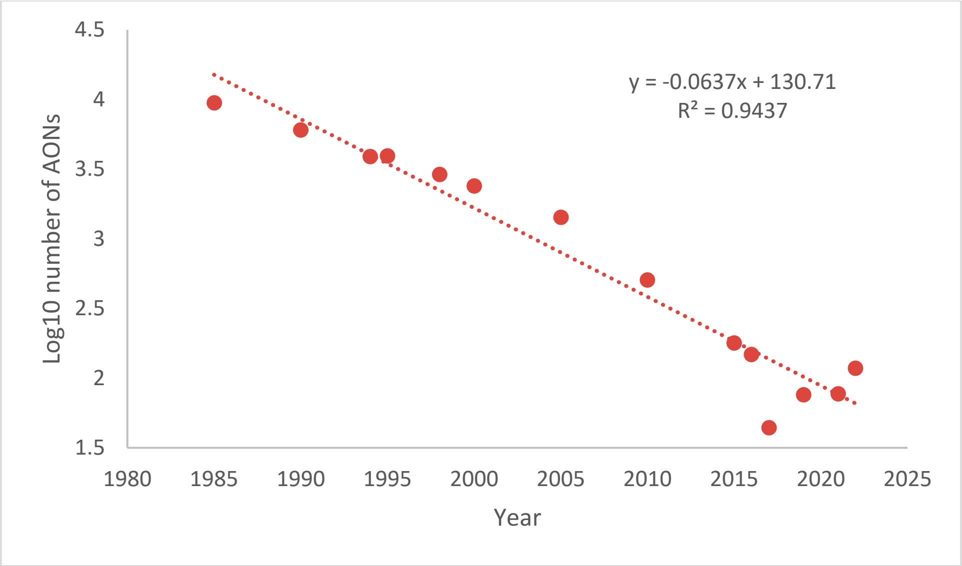

Figure 6. Log$_{10}$ of kittiwake AONs at Noss 1985-2022. Census data from JNCC Seabird Monitoring Programme online database with 2022 data from Miles *et al*. 2022.

74. These empirical data suggest either that there is no Allee effect in individual colonies of kittiwakes, or that any Allee effect only occurs once numbers are reduced by more than 99.5%, or that any Allee effect is hidden by other factors such as changes in mean nest site quality increasing as numbers decline. There is evidence for the last of these and the empirical evidence suggests that nest site quality effects may be considerably stronger than depensatory effects of predation.

75. Overall, the evidence for positive density-dependence in seabirds is very limited, most examples being related to increased risk of nest predation at low population size or nesting density. There is very little evidence to suggest that positive density-dependence acts on moderate or large seabird colonies. It may have an effect on small colonies, especially of terns as terns are highly vulnerable to nest predation. Empirical evidence suggests that for most seabird species positive density-dependence is likely to have less influence on rate of change in numbers than the effect of improvement in the average quality of occupied nest sites as a population is reduced (Potts *et al*. 1980, Werner *et al*. 2014, Bennett *et al*. 2022). For example, only 4% of all shag nest sites on the Farne Islands were considered to be entirely satisfactory, and nest site quality acted as strongly negatively density-dependent (Potts *et al*. 1980).

3.4 Empirical evidence for seabird populations at low numbers: sustainable or not?

76. Theoretical Allee effects include possible genetic effects and possible ecological effects of very small population size. There are examples of extremely rare seabirds that may inform whether these Allee effects can be detected in very small populations. This prompts

consideration of case studies of seabirds with very small population sizes to seek evidence for genetic or ecological Allee effects.

77. Several million pairs of short-tailed albatrosses *Phoebastria albatrus* bred in at least 14 colonies in the North Pacific Ocean off Japan in the late 19th century, but numbers were drastically reduced by harvesting and the species was declared extinct in 1949 (Sato *et al.* 2009, Finkelstein *et al.* 2010, Eda *et al.* 2020). However, a remnant population was discovered on Torishima Island in 1951, possibly derived from immature birds that escaped the harvest. There were only 23 birds in the population in 1954-55 which produced 7 eggs. Genetic analysis showed that about 1,000 years ago there were two very closely related species of short-tailed albatross and it was thought that only one of these survived, at Torishima Island. However, a very few breeding short-tailed albatrosses were found on the Senkaku Islands in 1971. These turn out to be of the second species, not the same as those on Torishima Island, so both these two species survived a close-to-extinction experience (Eda *et al.* 2020). Numbers at Torishima Island increased so that by 2014 the population there was estimated at 3,540 birds. A small group of birds from Torishima was translocated to the Bonin Islands to form a new colony, as the Torishima colony is on an active volcano and was considered at risk of extinction when the volcano erupted. In 2014 there were 10 birds in the Bonin Islands population, all derived from Torishima. All chicks at Torishima have been ringed each year, and yet ten unringed birds joined the colony at Torishima. Those birds, on genetic analysis, were found to be from the Senkaku Islands population of the sibling species, which by 2014 held 650 birds on the Senkaku Islands. Now both the two species of short-tailed albatross breed side-by-side on Torishima Island, while the second species breeds also on Senkaku Islands and the first also on Bonin Island (as a consequence of translocation). Birds from the two sibling species paired assortatively on Torishima, showing that these two species are indeed behaviourally distinct as well as genetically divergent. The key point in relation to possible Allee effects is that both these endangered sibling species of albatross have increased from a handful of birds to hundreds of birds of one species and thousands of the other, over a period of about 65 years. There has been no evidence of any adverse genetic effects that could be described as Allee effects (Kuro-O *et al.* 2010, Eda *et al.* 2020), and no evidence of any ecological Allee effects (Finkelstein *et al.* 2010). Clearly there was no strong Allee effect even though populations were reduced from millions of birds to fewer than 20 (Finkelstein *et al.* 2010, Eda *et al.* 2020).

78. The Amsterdam albatross *Diomedea amsterdamensis* was identified in the early 1980s as an extremely rare endemic species at Amsterdam Island, Indian Ocean, and probably the rarest seabird in the world. The breeding population comprised 42 birds in the early to mid-1980s with between 1 and 12 pairs breeding in different years (Jouventin *et al.* 1989). It is thought that the population was very much larger in the past and was reduced close to extinction by harvesting by sealers, whalers and fishermen, by habitat degradation by people living on the island, and by introduced rats, cats, dogs, pigs and cattle (Jouventin *et al.* 1989). Although the population is at risk of extinction from fishery bycatch (Weimerskirch *et al.* 1997), demographic data collected on the small population indicate that breeding success, immature survival, age of first breeding and adult survival are typical of large albatrosses, and do not show any clear evidence of any genetic or ecological Allee effect (Jouventin *et al.* 1989, Weimerskirch *et al.* 1997).

79. Band-rumped storm-petrels *Hydrobates castro* were once abundant in Hawaii but have been brought close to extinction by introduced mammal predators (Antaky *et al.* 2020). Nevertheless, despite the very large reduction in population and the species now being considered at risk of extinction in Hawaii, with the associated theoretical prediction of low genetic diversity, Antaky *et al.* (2020) found only very low levels of inbreeding and a high maintained genetic diversity in this population, despite small effective population size (mean estimate of 414 individuals). They concluded that there was no evidence to suggest any genetic Allee effect in this population despite the small effective population size. Antaky *et al.* (2020) noted that this conclusion is entirely consistent with findings regarding the population genetics of other rare, endangered, seabird species, namely Hawaiian petrel *Pterodroma sandwichensis* (Welch *et al.* 2012), Balearic shearwater *Puffinus mauretanicus* (Genovart *et al.* 2007), and Magenta petrel *Pterodroma magentae* (Lawrence *et al.* 2008).

80. Barau's petrel *Pterodroma baraui* was once abundant on Reunion Island but has been driven close to extinction by invasive rats and cats, by habitat modification and by artificial light pollution attracting fledglings (Danckwerts *et al.* 2021). Genetic analysis of two small remnant populations breeding 5 km apart in the central mountains of Reunion Island showed high genetic diversity in both populations despite small effective population sizes (550 and 1,200 individuals), no inbreeding, but significant genetic difference between the two populations (Danckwerts *et al.* 2021). The authors inferred that the genetic differences were the result of extremely high philopatry. They concluded that there was no evidence of any genetic Allee effect in either of these two populations, and that threats to these populations are introduced mammal predators and light pollution rather than genetic Allee effects, despite their small population size.

81. Although genetic Allee effects could (at least theoretically) arise as a result of seabird populations being reduced to very small numbers, the empirical evidence suggests that many seabird populations that have been reduced drastically in numbers close to extinction do not show any clear genetic Allee effects. Examples of seabirds recovering from a handful of breeding birds suggest that landscape-scale ecological factors that threaten seabird populations, such as prey-fish depletion, fishery bycatch of seabirds, introduced mammal predators at colonies, represent clear threats to seabird survival, and that depensatory density-dependent effects have little influence by comparison with these major landscape-scale impacts.

3.5 Barents Sea guillemot crash and recovery

82. The Barents Sea supports large stocks of cod, herring and capelin, all of which are the target of commercial fisheries. It also holds large populations of seabirds. In 1986-87 the capelin stock collapsed and there were also extremely low abundances of 0-group herring and 0-group cod. This two-year period was unique in having exceptionally low abundance of all three fish at the same time. About 90% of the common guillemots in the Barents Sea died, an exceptional catastrophic mortality that was linked to the exceptional shortage of suitable food for this piscivore specialist (Vader *et al.* 1990, Erikstad *et al.* 2013). Guillemot breeding numbers have been monitored in detail at Hornøya, north Norway and showed the crash in numbers in 1987 with a decrease of about 80% in common guillemot numbers (**Figure 7**), similar to that seen throughout the rest of the Barents Sea. In 1988 0-group herring abundance was higher, capelin abundance increased and 0-group cod abundance began to

increase slowly (Erikstad *et al.* 2013). Common guillemot breeding numbers at Hornøya slowly recovered and by 2005 had returned to the level present before the population crash (Figure 7). It took about 20 years for this population to recover from an 80% loss of breeding adults.

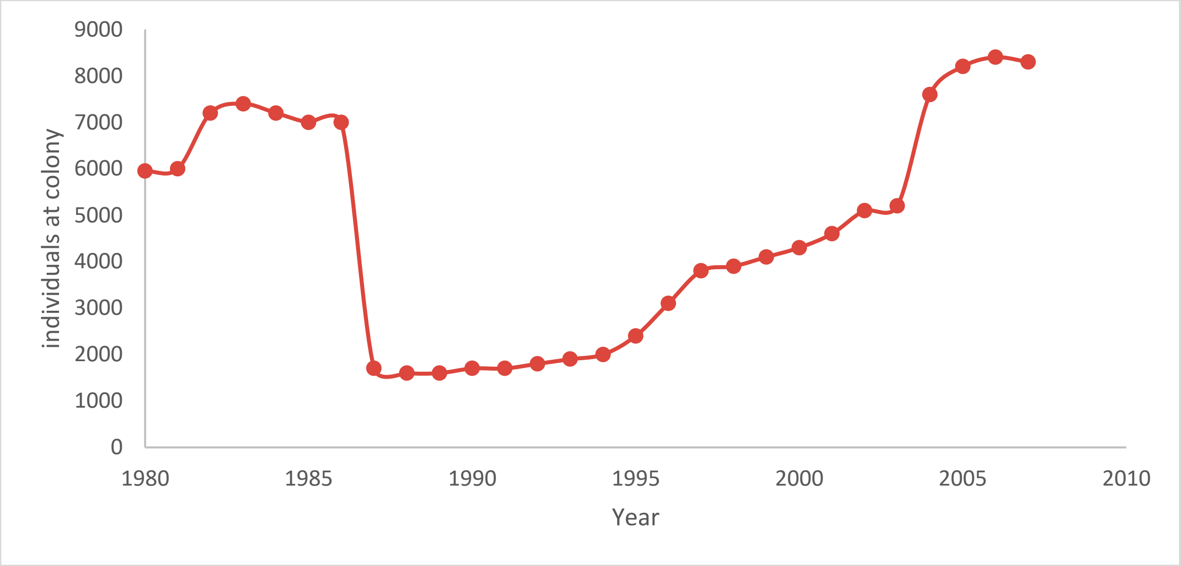

Figure 7. Number of common guillemots at Hornøya, north Norway 1980 to 2007. Data from Erikstad *et al.* (2013).

83. It would be reasonable to assume that the recovery of breeding numbers in Hornøya and throughout the Barents Sea during 1988-2005 occurred in an effectively closed population, as the birds in the Barents Sea are described as a distinct subspecies of common guillemot *Uria aalge hyperborea*. That subspecies is considerably larger than the subspecies found in Scotland (*Uria aalge aalge*) while another subspecies (*Uria aalge albionis*), which is even smaller and paler (browner) on the upperparts, breeds in southern Europe as far north as England and Ireland. There is also strong clinal variation in the proportion of common guillemots that are 'bridled' which is a genetic feature (bridled birds have a white eye-ring and white line behind the eye). Colonies further north have a much higher proportion of 'bridled' birds as well as having larger birds. These genetic differences suggest that there is little gene-flow between common guillemot populations, and therefore that the recovery of the Barents Sea '*hyperborea*' population would not involve immigration of guillemots from outside that area. Remarkably, we know from ringing that some birds from north Scotland moved to breed at colonies in the Barents Sea shortly after the population collapse occurred. A guillemot ringed as a chick at Shetland in 1990 was found breeding at Hornøya in 1994, and a second Shetland-ringed chick was found at a nearby southern Barents Sea colony at Vardø in 1995 (Pennington *et al.* 2004). There have also been examples of *aalge* guillemots moving to breed at colonies within the geographical range of *albionis* and vice-versa. It is interesting that chicks from Shetland moved to north Norway, as the collapse of the sandeel stock at Shetland in the late 1980s led to poor conditions there for seabirds dependent on sandeels as prey. However, since only a very small proportion of the guillemot chicks at Shetland are ringed each year, the fact that two are known to have moved to breed in the Barents Sea suggests that larger numbers of unringed birds from Shetland most likely also did that. How could Shetland guillemots become aware of the opportunity to join the Barents Sea

guillemot population at a time when food supply was improving but guillemot numbers were far below carrying capacity? Recent geolocator tracking of guillemots (Buckingham *et al.* 2022) found that a small proportion of guillemots from Shetland visit the Barents Sea in late summer to moult, which would give them the opportunity to assess the potential to breed there rather than to return to Shetland. This suggests that the recovery of the Hornøya common guillemot population, which took 20 years, might have taken even longer if immigration of birds from far away into the region had not been possible. However, this case study shows that common guillemot populations can be limited by food supply, that they can recover when food supply has recovered, and that recovery can occur even when the regional population has been reduced by as much as 80-90%.

3.6 Historical evidence on population change in great skua and gannet

3.6.1 Great skua

84. Great skua numbers are relatively well documented since the 18th Century because this has been a rare species of interest to naturalists visiting remote areas where it breeds. Although always a relatively scarce species because it is a top predator, the great skua was severely reduced in numbers in the late 19th century by human harvesting of eggs and chicks but mainly by shooting of adults for museum collections (Furness 1987). Harvesting of eggs and chicks by local people may have been sustainable, but shooting by collectors from Britain, Germany and elsewhere was not. The great skua population in the Faeroe Islands was reduced to about 36 pairs in 1872, and by 1897 was down to just four pairs, each of the four pairs nesting on a different island (Furness 1987). Many of the birds shot in the 1870s to 1890s are now in collections in major museums such as the British Museum of Natural History, the Copenhagen Natural History Museum, the National Museums of Scotland. In December 1897 an Act of Parliament was passed in the Faeroes that gave protection to the great skua. Numbers then recovered as visiting shooters from overseas were unable to get to the remaining birds in the Faeroes. The population increased to 71 breeding pairs in 1930, occupying all four of the sites where just a single pair had remained at each in 1897 (Furness 1987). There were 530 pairs of great skuas in the Faeroes in 1961 (Bayes *et al.* 1964), 500 pairs in 1977 (Furness 1987), 270 pairs in the 1980s-1990s (Mitchell *et al.* (2004), and 500 pairs in 2010 (Hammer *et al.* 2014). Furness (1987) concluded "*the history of the great skua in the Faeroe Islands suggests that great skuas are surprisingly capable of increasing from very low numbers despite the devastation that can be caused by shooting*".

85. The history of great skuas in Scotland is similar to that in the Faeroes. In 1774 great skuas only nested at two sites in Scotland, both in Shetland; three pairs nested at Saxavord on Unst, and six or seven pairs high on the hills of Foula (Furness 1987). Numbers increased at Foula to 30 pairs in 1804, but during the early 19th century taxidermists began to visit Shetland to shoot great skuas. By the 1880s conservationists argued that the species was likely to be lost from Scotland as a result of uncontrolled and excessive shooting pressure. The near-extermination of great skuas and the success story of protection by volunteer wardens of the few pairs left at Hermaness and Foula, played an important role in promoting the formation of a protection of birds society and in developing legislation to protect birds. After 1900, great skua numbers increased at an almost constant rate of 7% per annum at Foula, reaching 3,000 pairs in 1975 (Furness 1987). It is likely that the growth was encouraged by provision of large volumes of fishery discards from trawlers fishing for whitefish around Shetland and other parts of

Scotland, as discards form an important part of the diet of breeding great skuas (Votier *et al*. 2004, Church *et al*. 2018). The much greater increase in numbers in Shetland compared to the Faeroes may reflect the high volumes of discards provided around Shetland in the 1950s-1970s, much greater than was ever the case around the Faeroes. Ringing of great skua chicks at Foula showed that new colonies that developed in other areas of Shetland, in Orkney, Western Isles and mainland Scotland were founded by birds that included chicks fledged from Foula, as were new colonies founded in Norway (including Bear Island and Spitsbergen) and north Russia (Furness 1987). Many new "colonies" were initially colonised by a single pair of great skuas, with numbers then increasing over following decades. For example, 1 pair took up territory on Hirta, St Kilda, in 1956, and only one pair nested there in 1963, and 1965, but there were 3 pairs in 1965, 5 or 6 pairs in 1968, 6 in 1969, 8 in 1971, 8 in 1972, 9 in 1974, 15 in 1975, 20 in 1976, 22 in 1977, 25 in 1978 (Harris and Murray 1978). One pair nested on Noss, Shetland in 1913 and 1914, increasing to 20 pairs in 1946 (Perry 1948). One pair nested on Hoy, Orkney, in 1914, 1915, 1916, 1917 increasing to 4 pairs in 1921, 8 in 1933, 20 in 1941, 70 in 1961, 462 in 1975 (Furness 1977). One pair nested at Handa in 1964, 1 in 1965, 2 in 1966, 3 in 1967, 1968, 1969, 1970 and 1971, 4 in 1972, 5 in 1973, 7 in 1974 (Furness 1977). Clearly great skua colonies can often start from a single pair and may take some years for numbers to build up.

86. The national breeding seabird census in 2000 found a population of 9,600 pairs of great skuas in Scotland (Mitchell *et al*. 2004). Between 2000 and 2019, numbers increased at most small colonies but decreased at some of the largest colonies (**Figure 2**). The decreases that occurred at the largest colonies were associated with low breeding success, increased age of first breeding and reduced survival associated with the collapse of the Shetland sandeel stock in the early 1980s and reduced volumes of whitefish discards that occurred mostly in the 1980s and has continued to be reduced since then. The provision of a discards food subsidy to great skuas for several decades probably allowed the population to grow to a level that is unsustainable in an environment with a zero-discard fisheries policy. Special Protection Areas established with breeding great skua as a feature were mostly designated in the 1990s, at a time when great skuas were close to their all-time highest breeding numbers in Scotland since the early 1700s. HPAIV has killed very large numbers of adult great skuas in 2021 and especially in 2022, and is likely to see populations in SPAs fall further below the numbers that were present at designation, but there is a case to be made that this has simply accelerated a process of decline in size of the largest colonies towards a better fit with reduced environmental carrying capacity for this species (although that argument probably has no traction in relation to Birds Directive legal requirements to maintain features of SPAs unless reduced carrying capacity after removal of an anthropogenic food subsidy is considered to be part of 'natural change').

3.6.2 Gannet

87. The gannet is relatively easy to census because there are not very many colonies of this species, it nests in well-formed nests in the open that are generally closely-packed with other neighbouring gannet nests, one of the adults is normally on the nest throughout the breeding season from April to September, and breeding success in this species is generally high in all years in all colonies, so that attendance remains consistent throughout almost all of the breeding season (Nelson 1978). In 1939 two ornithologists coordinated a census of all the world's northern gannet colonies (Fisher and Vevers 1943-44) and that census has been repeated every ten years since at all Scottish colonies and in most decades at all North

Atlantic colonies. All Scottish colonies were counted in 2013-14, with 243,505 AOS and an average rate of increase of 2.9% per annum from 2004 to 2014 (Murray *et al.* 2015). Icelandic colonies were counted in 2013-14, with 37,000 AOS so an annual increase of 1.88% over recent decades (Gardarsson 2019). North Norwegian colonies were counted in 2015-16 with 3,300 AONs, increasing at an average rate of 3% per annum from 2008 to 2016 (Barrett *et al.* 2017). Including the colony at Runde in southern Norway, the Norwegian population in 2015-16 was 6,900 AONs, up from 3,700 in 1995 and 4,500 in 2008 (Barrett *et al.* 2017). North American colonies in 2009 held 116,825 pairs with an average growth rate from 1984 to 2009 of 4.4% per annum but slowing in the later part of this period most likely due to density-dependent competition for food (Chardine *et al.* 2013). Many individual colonies have been counted again since those coordinated surveys so that population data for gannet are exceptionally detailed and accurate as well as covering an exceptionally long time period.

88. Formation of new colonies by gannets tends to be a slow process, often with large numbers of immature birds aggregating at a potential new colony site each summer for some years before birds start to nest, as seen at Fair Isle (Nelson 1978) and Foula (Furness 1981). At some colonies several pairs nested in the first year of breeding at the new colony, but some new colonies have been founded by just one pair with very slow initial growth. Nelson (1978) describes the very slow start to colony growth at Great Saltee and at Bempton. At Great Saltee one (or possibly two) pairs nested in 1929. There were still only 1 or 2 pairs until 1949 when a third pair nested. In 1954 there were 4 pairs, in 1955 8 pairs, in 1956 17 pairs, in 1960 60 pairs and in 1973 200 pairs (Nelson 1978). At Bempton one (or possibly two) pairs nested in 1929, 2 pairs in 1934, 2 pairs in 1939, 2 pairs in 1951, 12 pairs in 1954, 18 pairs in 1959, 26 pairs in 1964, 30 pairs in 1969, 33 pairs in 1971, 44 pairs in 1972, 100 pairs in 1974, 120 pairs in 1975 (Nelson 1978). Bear Island was colonised by only two pairs in 2011, and 2 pairs nested there in 2012, but the numbers increased to 10 pairs in 2013, 11 in 2014, 25 in 2015 and 52 in 2016 (Barrett *et al.* 2017), the relatively rapid growth clearly being due to immigration as chicks produced at Bear Island would not be old enough to breed during the first few years of colony growth. Kharlov, north Russia, was colonised by one pair of gannets in 1995, and one pair nested in 1996, but the colony grew to 19 pairs in 1997, 18 in 1998, 16 in 1999, 22 in 2000 and 2001, 48 in 2002, 30 in 2004, 145 in 2005, 161 in 2006, 232 in 2007 (Barrett *et al.* 2017).

89. The ability of gannet colonies to grow from just one or two pairs reflects the high adult survival of this species and the fact that it is not subject to much predation impact while breeding – in part because of its large size so that gulls and crows are unable to access nests defended by an adult gannet unless the adult is displaced by human disturbance (Nelson 1978). The general increase in gannet populations will also mean that there is a pool of immature nonbreeding birds seeking to find nest sites so likely to join growing colonies. However, gannets can be subject to predation by white-tailed eagles. In Norway, the increasing population of white-tailed eagles has led to declines in gannet numbers at a few colonies, but the affected colonies are not necessarily small ones. For example, the two largest gannet colonies in the Lofoten/Versterålen region were abandoned by gannets as a result of harassment by white-tailed eagles (Barrett *et al.* 2017). Despite local effects of white-tailed eagles, the regional population of gannets continued to increase, and there was no evidence to suggest that impacts of eagles inhibited population growth or the formation of new colonies (Barrett *et al.* 2017).

4 POSSIBLE RESPONSES OF SEABIRDS IN THE NORTH OF SCOTLAND TO THE HPAI EPIDEMIC

90. The seabirds in north Scotland most severely affected by HPAIV in 2021 and 2022 breeding seasons were great skua and gannet. Towards the end of the 2022 breeding season an impact on common guillemots started to become evident at a few colonies and more widely from beached birds on coasts, both in east and west Scotland, but apparently not so much in Shetland or Orkney. The HPAIV outbreak in Newfoundland in 2022 apparently hit common guillemots much harder than it did in the UK, and apparently hit guillemots harder than gannets (Bill Montevecchi, pers. comm.). There might well be further mass mortality of UK seabirds from HPAIV in 2023 and beyond, and a heavy toll on common guillemots might be anticipated given their dense packing on nesting ledges.

91. Predicting what will happen in 2023 is extremely difficult as this virus is novel in colonial seabirds. Immunity to HPAIV may arise in some or most populations of our seabirds, reducing long-term impacts. Experimental infection of tufted ducks and mallards in the laboratory showed that birds given a low pathogenicity infection developed protective immunity that protected against experimental infection with HPAIV nine months later (Caliendo et al. 2022b). It is uncertain if HPAIV will have created immunity in a significant proportion of the survivors in populations worst hit by the virus in 2022. However, it would not be a surprise if the 50% or greater mortality of UK great skuas and Dutch Sandwich terns in 2022 might be followed in 2023 by similar mass mortality of other seabird species. In Scotland we can anticipate likely further outbreaks in great skuas and gannets as well as spread to other seabird species.

4.1 Great skua

92. Shortly before the HPAIV epidemic, great skua SPA feature status was classified by NatureScot as Favourable Maintained at all but one of the Scottish SPA network sites for breeding great skua, although numbers had decreased at three sites; Foula, Hoy, and St Kilda (**Table 1**).

Table 1. Summary of great skua breeding SPA feature conservation status up to 2019

SPA	Pairs in citation	Most recent published count	Change from designation	Percent change	SCM
Hermaness, Saxa Vord & Valla	788	955 in 2018	+167	**+21**	FM
Fetlar	508	743 in 2017	+235	**+46**	FM
Foula	2,270	1,846 in 2015	-424	**-19**	FR
Ronas Hill	130	289 in 2017	+159	**+122**	FM
Noss	420	476 in 2018	+56	**+13**	FM
Fair Isle	110	490 in 2019	+380	**+345**	FM
Hoy	1,900	1,063 in 2019	-837	**-44**	UD
Handa	66	283 in 2018	+217	**+329**	FM

SPA	Pairs in citation	Most recent published count	Change from designation	Percent change	SCM
St Kilda	270	179 in 2012-19	-91	-34	FM

93. The deaths of a minimum of 1,500 adult great skuas at Foula in summer 2022 (Camphuysen and Gear 2022) can be considered equivalent to the loss of at least 750 pairs from this colony, as evidence from ring numbers on dead birds was that dead birds were likely to be of breeding age. Putting this into context, it took about 65 years for the colony to grow from tens of pairs in 1890 to 750 pairs (around 1955), but less than 10 years to increase from 2,000 pairs in the early 1970s to 3,000 pairs in the late 1970s (Figure 8). The time required for population recovery depends on how much the population is reduced. Not only does it take longer to recover from a larger impact, but it also takes longer to recover from a smaller starting size than from a larger starting size. How quickly the population can recover will depend in part on the size at which it ends up after HPAIV has taken its toll. The time to recovery will also depend on the extent to which negative (compensatory) density-dependence results in higher survival, younger age of first breeding and increased breeding success in a smaller post-HPAIV population, and on the extent to which carrying capacity might change as a result of landscape-scale changes in food availability and impacts of climate change. Breeding numbers of great skuas at Foula had been declining gradually from 1977 to 2015 (Figure 9), and this is interpreted as a response to a reduced carrying capacity, especially in relation to availability of sandeels and fishery discards at Shetland.

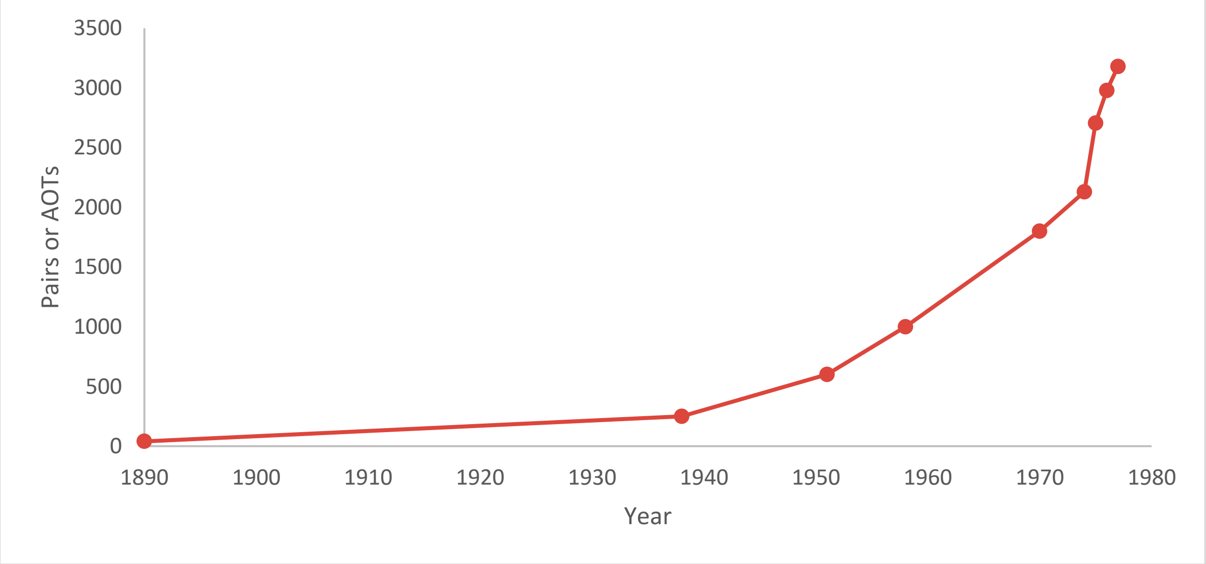

Figure 8. Numbers of great skua pairs or AOTs at Foula, 1890 to 1977.

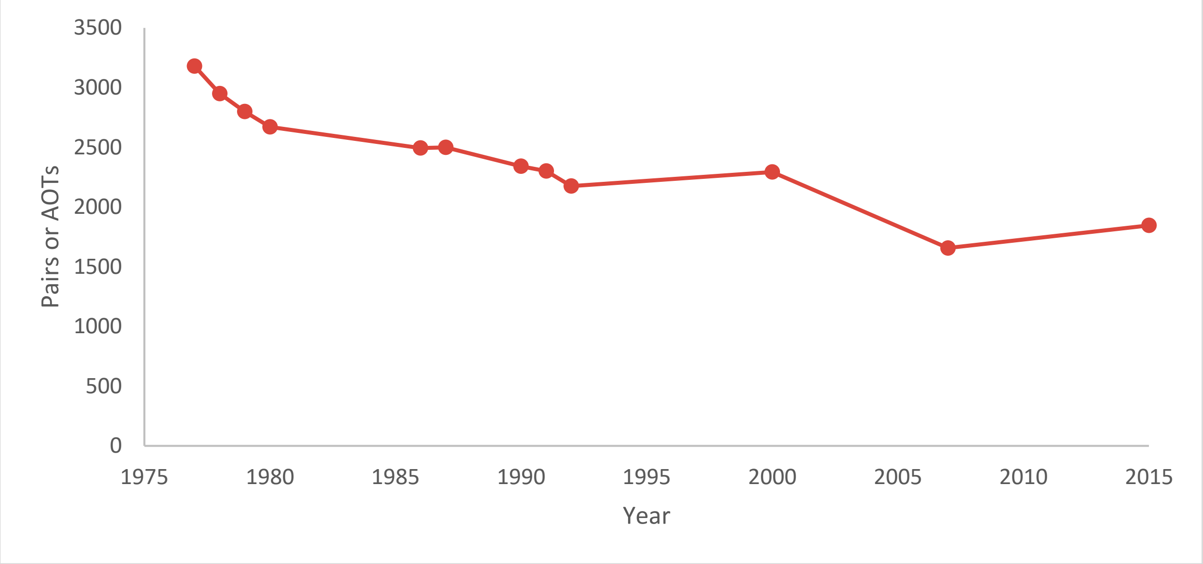

Figure 9. Numbers of great skua pairs or AOTs at Foula, 1977 to 2015.

94. As discussed earlier, it is likely that the carrying capacity of great skuas in northern Scotland was increased artificially by provision of fishery discards, and that the changes to fishery management since the 1970s (a combination of changed technical measures such as net mesh size, and legal measures such as total allowable catches and limits on discarding towards a zero-discard policy) will have progressively reduced the carrying capacity for great skuas in the region. Since SPAs with great skua as a breeding feature were established around the time when great skua breeding numbers were at their peak at the largest colonies (but still increasing at almost all smaller colonies), it is likely that even without the HPAIV outbreak great skua breeding numbers at some or most Scottish SPAs with this species as a breeding feature would in future fall below the numbers at site designation. Breeding numbers of great skuas increased by an average of 23% (median 10%, range -40% to +200%) between 2000 and 2019 at the nine colonies designated as SPAs for breeding great skua (Furness 2022). At colonies that were not SPAs for breeding great skua the change in the same time period was +221% (median 240%, range -40% to +600%). This difference is statistically significant (Mann-Whitney U = 26, $p<0.05$), showing a higher growth in the smaller colonies. The impact of HPAIV is likely to take some or most of the SPA populations below the numbers where the site will be assessed as in unfavourable conservation status for breeding great skua if that assessment is based simply on breeding numbers rather than considering HPAIV as part of 'natural change'. It is difficult to see how HPAIV could be considered 'natural change' as this virus originated in intensive chicken farms and only spread to seabirds from outbreaks in domestic birds, so this impact on seabirds is anthropogenically-derived rather than part of the natural environment of seabirds.

95. Even if HPAIV has no further impact on great skuas in northern Scotland (which seems improbable) it will probably take 20 years or more for numbers to recover from the impact of HPAIV in 2021 and 2022. A more likely scenario may be that it will take even longer than that and that numbers at the largest colonies may never recover to 1980-2000 numbers because of the reduced carrying capacity for this species, with most recovery occurring in small colonies. If further HPAIV outbreaks occur then the medium-term changes in great skua

numbers may depend on the extent to which birds develop immunity to the infection, but it is possible that smaller colonies may be slightly more likely to escape reinfections than would the larger and denser colonies. Unfortunately, we cannot be confident in predicting any of these scenarios at this stage, but perhaps the most likely will be a long-term reduction in numbers of great skuas at large colonies but some further colonisation of new sites with establishment of small colonies that grow more than the largest ones do.

4.2 Gannet

96. All gannet colonies in Scotland have been increasing, though some colonies have recently increased much more than others (Table 2). Shortly before the HPAIV epidemic, gannet SPA feature status was classified by NatureScot as Favourable Maintained at all eight of the Scottish SPA network sites for breeding gannet. The SPA colonies in Scotland held about 95,000 pairs more in 2013-2019 than they did at SPA designation (Table 2). This suggests that the HPAIV mortality at gannet colonies in 2022 is unlikely to have reduced breeding numbers below the numbers present at SPA designation as the total mortality of adult gannets from Scottish colonies in 2022 is likely to have been many tens of thousands of individuals, but probably not in excess of 190,000. However, this remains uncertain and further evidence from beached bird surveys, migration counts at coastal sites, and counts of gannet AOS at colonies in 2023 will be needed to get a better understanding of the scale of mortality.

Table 2. Summary of gannet breeding SPA feature conservation status up to 2019.

SPA	Pairs in citation	Most recent count	Change from designation	Percent change	SCM
Ailsa Craig	23,000	33,226 in 2014	+10,226	**+44**	FM
Fair Isle	1,166	4,211 in 2019	+3,045	**+261**	FM
Forth Islands	21,600	75,259 in 2014	+53,659	**+248**	FM
Hermaness, Saxa Vord & Valla	16,400	25,580 in 2014	+9,180	**+56**	FM
North Rona & Sula Sgeir	10,400	11,230 in 2013	+830	**+8**	FM
Noss	6,860	13,765 in 2019	+6,905	**+101**	FM
St Kilda	50,050	60,290 in 2013	+10,240	**+20**	FM
Sule Skerry & Sule Stack	5,900	6,420 in 2013	+520	**+9**	FM

97. It is likely that breeding numbers of gannets will be significantly reduced at most Scottish colonies as a result of HPAIV impact on gannets in 2022. Breeding success of gannets was exceptionally poor in 2022, but that is unlikely to play any important role in the population dynamics. Survival of gannets through the first few weeks of life is low, and the loss of just

one or a few cohorts will have little implication in terms of potential recruitment of four to six year old birds into colonies. Decreases in numbers are likely to be driven almost entirely by mortality of adults.

98. Whereas many or most great skuas that died were to be found at colonies, often in communal areas where birds bathe/preen, many dead gannets appeared on beaches. Although numbers of dead gannets were especially high on beaches close to major colonies, there were large numbers of dead gannets on beaches throughout the British Isles and on the continental coast of the North Sea, even into the Norwegian Sea and Baltic Sea. That makes estimating the impact of HPAIV on gannets more difficult. It is entirely possible that the impact might reduce gannet breeding numbers by 50% or more, but this will not be evident for at least one or more years, depending on whether gannets develop resistance to HPAIV and return to 'normal' breeding, or whether breeding is disrupted in future years by adult mortality from HPAIV and consequent abandonment of nest sites by many of the surviving gannets. Counts of breeding numbers cannot be considered reliable if high proportions of the breeding population choose to leave or not to return to nest sites.

99. Analysis of the Trektellen online data[2] on gannet numbers observed passing coastal observation sites (e.g. **Figure 10**), and analysis of beached bird survey data on numbers of dead gannets, may help to improve understanding of HPAIV impact on the gannet population, but it is difficult to know how to interpret changes in numbers in those data sets in terms of evidence for change in population size rather than bird behaviour.

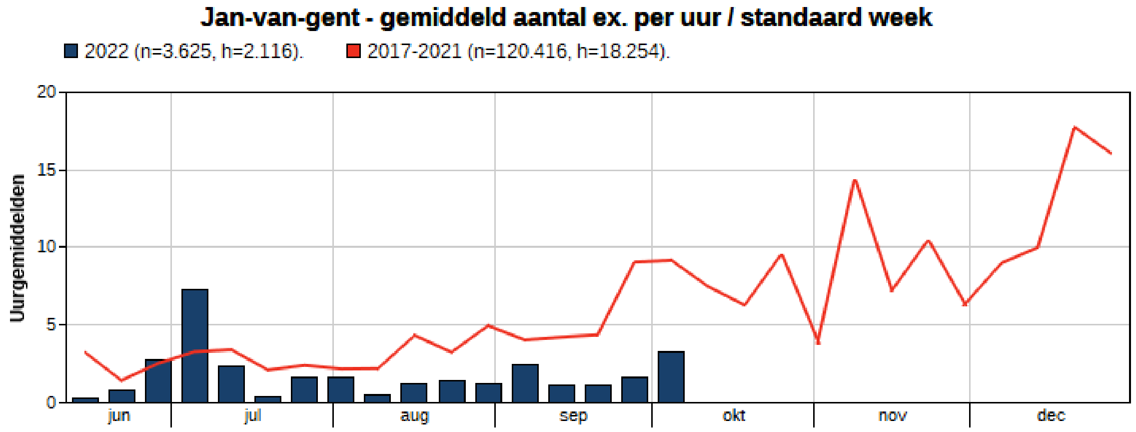

Figure 10. Gannet numbers observed at seawatching sites in The Netherlands in 2022 (blue histogram) compared to the average numbers in 2017-2021. The data suggest an early departure of gannets in early July but much lower numbers in August-October than in 'normal' years. Data provided by Kees Camphuysen from the Trektrellen online database.

100. It may be possible to obtain estimates of numbers of gannets that died at sea from HPAIV in summer 2022 from the SCANS IV aerial surveys (which target mapping of porpoises but in 2022 also included mapping of dead gannets seen from transects throughout UK waters in July-August). Any such estimates would be likely to be in the low thousands but would have to make various assumptions about the proportion of dead gannets that are on the water

---

[2] https://www.trektellen.org/

rather than washed up on shores, and on how long corpses float on the surface before sinking or decomposing.

101. If gannets do develop resistance to HPAIV then it would be reasonable to expect gannet breeding numbers to resume their increase at a similar rate to that seen for several decades before HPAIV arrived. However, there was very little evidence of compensatory density-dependence affecting gannet population growth. Growth rate of the total population had declined slightly over recent decades, suggesting possible density-dependence as numbers trended towards carrying capacity, but some of the fastest growing colonies included very large ones such as Bass Rock. Foraging trips by breeding gannets were longer at larger colonies, consistent with compensatory density-dependence. However, breeding success showed no clear variation with colony size and no clear evidence has been found of difference in adult survival rate between colonies of differing size. This suggests that gannets had not yet reached carrying capacity, and therefore that growth rate of a population reduced by HPAIV may not benefit from any significant compensatory density-dependent gains to demographic parameters in this species.

4.3 Guillemot

102. Guillemot is a breeding feature of 30 SPAs in Scotland, 5 in Shetland, 6 in Orkney, 7 from Caithness to Berwickshire, 12 in the west of Scotland (**Table 3**). Shortly before the HPAIV epidemic, guillemot SPA feature status was classified by NatureScot as Favourable at 11 of the Scottish SPA network sites for breeding guillemot, but Unfavourable at 19 (**Table 3**). Unfavourable conservation status was especially clear at colonies in Shetland, where the collapse of the local sandeel stock in the 1980s can be considered a contributory factor to reducing local carrying capacity but was also evident at colonies in Orkney and much of north and north-west Scotland (**Table 3**). Colonies with Favourable conservation status tend to be in eastern, south-eastern or south-western Scotland (**Table 3**).

Table 3. Summary of common guillemot breeding SPA feature conservation status in Scotland up to 2019

SPA	Individuals in citation	Most recent published count (individuals)	Change from designation	Percent change	SCM
Hermaness, Saxa Vord & Valla	25,000	6,109 in 2016	-18,891	-76	UD
Noss	38,970	24,456 in 2015	-14,514	-37	UNc
Foula	37,500	24,799 in 2007	-12,701	-34	UD
Sumburgh Head	16,000	7,749 in 2018	-8,251	-52	UD
Fair Isle	32,300	20,924 in 2015	-11,376	-35	UD
West Westray	42,150	28,697 in 2017	-13,453	-32	UD
Calf of Eday	12,645	5,524 in 2018	-7,121	-56	UD
Rousay	10,600	6,500 in 2016	-4,100	-39	UD
Hoy	13,400	12,198 in 2017	-1,202	-9	UNc

SPA	Individuals in citation	Most recent published count (individuals)	Change from designation	Percent change	SCM
Marwick Head	37,700	11,985 in 2018	-25,715	**-68**	UD
Copinsay	29,450	18,454 in 2015	-10,996	**-37**	UNc
North Caithness Cliffs	38,300	25,000 in 2016	-13,300	**-35**	FM
East Caithness Cliffs	106,700	149,228 in 2015	-42,528	**-40**	FM
Troup, Pennan and Lion's Hd	44,600	23,800 in 2017	-20,800	**-47**	UD
Fowlsheugh	56,450	69,828 in 2018	+13,378	**+24**	FM
Buchan Ness to Collieston	8,640	29,187 in 2019	+20,547	**+238**	FM
Forth Islands	16,000	25,956 in 2018	+9,956	**+62**	FM
St Abb's Head to Fast Castle	31,750	43,000 in 2018	+11,250	**+35**	FM
Cape Wrath	13,700	38,109 in 2017	+24,409	**+178**	FM
North Rona & Sula Sgeir	43,200	4,961 in 2012	-38,239	**-89**	UD
Sule Skerry & Sule Stack	6,298	10,068 in 2018	+3,770	**+60**	FM
Handa	98,686	54,664 in 2016	-44,022	**-45**	UNc
St Kilda	22,700	10,300 in 2016	-12,400	**-55**	UD
Mingulay & Berneray	30,900	22,265 in 2014	-8,635	**-28**	FR
Flannan Isles	21,930	9,807 in 2000	-12,123	**-55**	UD
Canna and Sanday	5,800	2,850 in 2018	-2,950	**-51**	UD
Rum	4,000	2,454 in 2000	-1,546	**-39**	UNc
Shiant Isles	18,380	9,054 in 2015	-9,326	**-51**	UNc
North Colonsay & Western Cl	6,656	18,724 in 2018	+12,068	**+181**	FM
Ailsa Craig	3,350	6,180 in 2019	+2,830	**+84**	FM

103. Additional adult guillemot mortality caused by HPAIV is likely to move some of the SPA breeding guillemot populations that have been in Favourable conservation status towards Unfavourable conservation status, and to move some in Unfavourable status to being further depleted. The extent to which this will occur is not yet clear. Guillemot mortality in 2022 seems only to have been evident towards the time when birds were leaving colonies. It is unclear if chick mortality in 2022 was due directly to HPAIV, or to birds starving because a

parent had died from HPAIV or had deserted the colony, or to other factors such as low sandeel abundance in 2022. The risk that large numbers of guillemots packed closely together on nesting ledges may die from HPAIV in the 2023 breeding season seems potentially high but remains uncertain.

4.4 Other species

104. It is to be hoped that seabirds that nest at relatively low density and do not interact in dense gatherings at foraging sites or at social and bathing sites may avoid high infection and high mortality from HPAIV in 2023 and following seasons. It seems likely that there will be a significant impact of HPAIV on kittiwakes given their relatively dense nesting and the risk of infected droppings falling from one nest onto others below. Similarly, tern colonies appear to be at high risk of virus transmission, although most Scottish tern colonies were apparently little affected by HPAIV in 2022 (but tern colonies at Farnes SPA, Coquet Island SPA, North Norfolk Coast SPA and colonies in The Netherlands were badly hit). It may be relatively difficult to detect impacts of HPAIV in seabirds that are cryptic such as nocturnal burrow-nesting petrels and Manx shearwaters. There will be an urgent need for increased monitoring in such species. It had been assumed that seabirds most at risk of HPAIV would be scavenging species likely to feed from carcasses of wildfowl that had died from HPAIV. There is little evidence this is the case, and it seems more likely that transmission has primarily been from bird to bird during close physical contact, especially at colonies but presumably also at sea during foraging. In that case, flock foraging may increase the chances of transmission of HPAIV.

105. There would be merit in assessing the extent to which apparently healthy seabirds at colonies in Scotland in 2023 and subsequent seasons show antibody responses to HPAIV and so are likely to have some immunity; that monitoring is urgently required in order to understand how soon seabird populations may become resistant to the HPAIV mass mortality events seen in 2022. It is to be hoped that SNCBs and the APHA lab will work together to determine levels of immunity to HPAIV in seabird populations.

5 HPAIV EVIDENCE AT WEST OF ORKNEY WINDFARM

106. The impact of the HPAIV epidemic on gannets and great skuas recorded for the baseline site characterisation data used in the West of Orkney Windfarm (the ‘Project’) Offshore Environmental Impact Assessment (EIA) Report and Offshore Report to Inform Appropriate Assessment (RIAA) was reviewed.

107. Baseline data was collected within the offshore ornithology survey area for the offshore Project by HiDef Aerial Surveying Limited using digital aerial survey methods (video cameras) over 27 surveys between July 2020 to September 2022. For further details of the baseline surveys, refer to the Supporting Study 8: Digital video aerial survey methodology and marine mammal survey results.

108. Digital aerial survey (DAS) data recorded the following information: species of each bird observation, count (number of individuals), behaviour either alive (flying, sitting on the sea) or dead, position (longitude and latitude coordinates) and a date and time stamp.

109. Dead birds were recorded for three bird species within the offshore ornithology survey area over the 27 surveys; a total of 31 dead gannets and one dead great skua and fulmar each were recorded.

110. **Figure 11** shows the number of individual alive and dead gannets recorded in each survey within the offshore ornithology survey area; dead gannets were recorded much more frequently in August and September 2022 than in any other month, prior to October 2021, no dead birds were recorded during DASs. Fewer alive gannets were recorded in August and September 2022 compared with the same months in 2021 and 2020.

111. **Figure 12** shows the number of individual alive and dead great skuas recorded in each survey within the offshore ornithology survey area; the number of skuas recorded each month was highly variable between years with no clear decline in 2022.

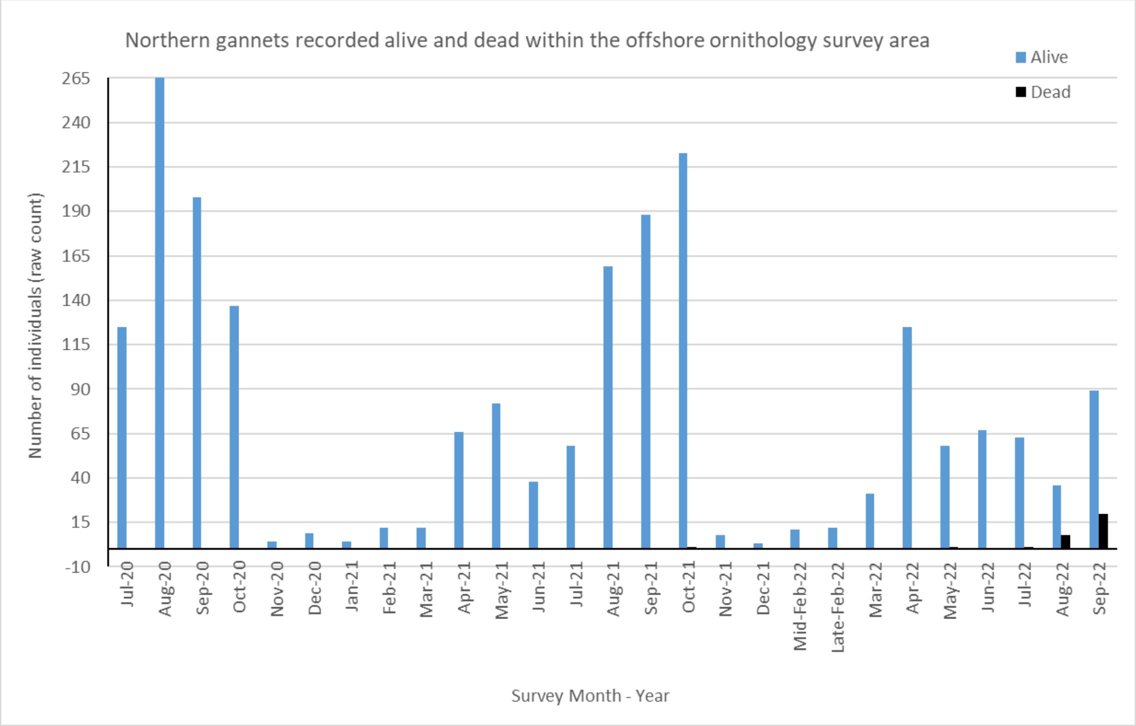

Figure 11. Gannet raw count data showing the number of individual alive and dead birds recorded in each survey.

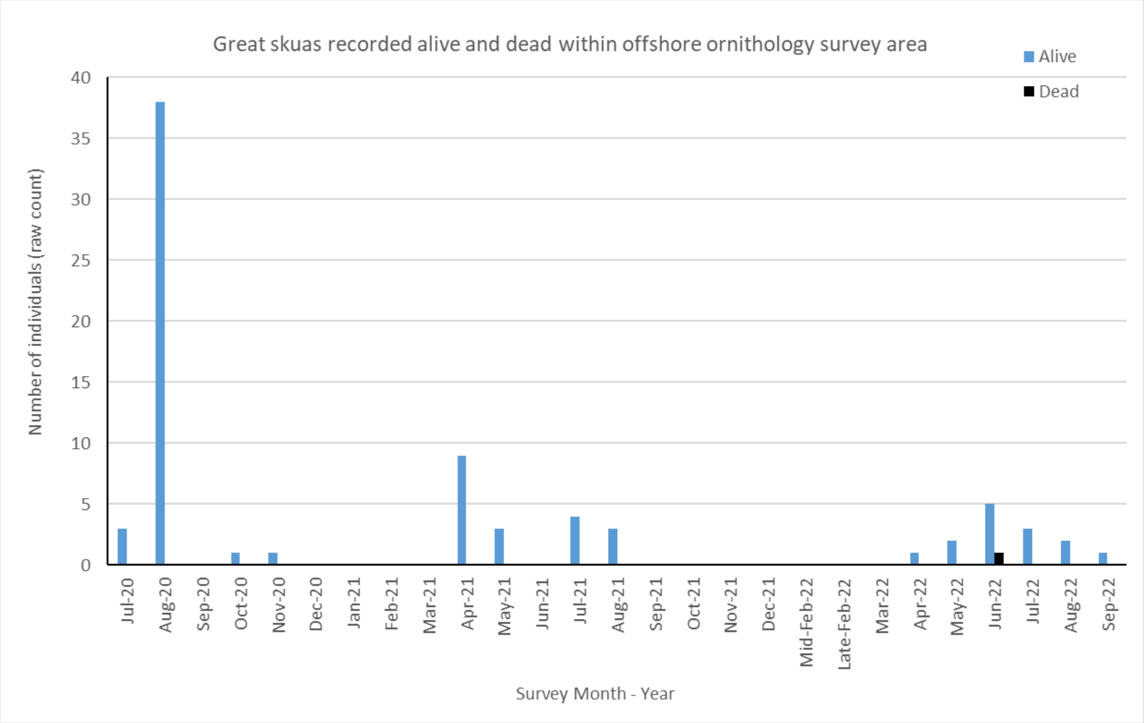

Figure 12. Great skua raw count data showing the number of individual alive and dead birds recorded in each survey.

112. As a decline in raw count data was recorded for gannet in August and September 2022, the mean abundance and density estimates of gannets used in the displacement and collision risk assessments for the months of August and September were compared with and without the comparable 2022 data (**Table 4** and **Table 5**).

113. For further information about abundance and density estimates used in the Offshore EIA and Offshore RIAA, refer to the Supporting Study 12: Offshore ornithology technical supporting study, Annex 12.3 (displacement assessment) and Annex 12.5 (collision risk assessment) for details.

114. Due to the overlap in confidence intervals, it is clear that there is no significant difference between the August and September abundance (**Table 4**) and density (**Table 5**) estimates when the August and September 2022 data is added or removed.

Table 4. Mean abundance (number of individuals) of all gannets in flight and on the sea, standard deviation (S.D.) and confidence intervals (95% c.i.,) in the Option Agreement Area and 2 km buffer estimated for August and September. Abundance is estimated with and without data collected in August and September 2022.

	Mean abundance			
Month	With August and September 2022 data		Without August and September 2022 data	
	Estimate (S.D.)	95% c.i.	Estimate (S.D.)	95% c.i.
August	958.12 (477.89)	318.11-2070.05	1331.84 (697.46)	406.93-2960.71
September	902.28 (116.67)	679.07-1135.98	1084.66 (132.09)	828.99-1344.31

Table 5. Mean density (birds/km2) of all gannets in flight, standard deviation (S.D.) and confidence intervals (95% c.i.,) in the Option Agreement Area estimated for August and September. Abundance is estimated with and without data collected in August and September 2022.

	Mean density			
Month	With August and September 2022 data		Without August and September 2022 data	
	Estimate (S.D.)	95% c.i.	Estimate (S.D.)	95% c.i.
August	0.36 (0.13)	0.17-0.65	0.49 (0.1)	0.32-0.7
September	0.66 (0.1)	0.47-0.88	0.78 (0.15)	0.51-1.08

REFERENCES

Alfarwi, I. 2022. The avian flu outbreak on Coquet Island, Northumberland. Seabird Group Conference, Cork. Surveillance and monitoring responses to Highly Pathogenic Avian Influenza, a workshop at Cork Seabird Conference (2022) - YouTube

Antaky, C.C., Conklin, E.E., Toonen, R.J., Knapp, I.S.S. and Price, M.R. 2020. Unexpectedly high genetic diversity in a rare and endangered seabird in the Hawaiian Archipelago. PEERJ 8: e8463.

Ashbrook, K., Wanless, S., Harris, M.P. and Hamer, K.C. 2010. Impacts of poor food availability on positive density dependence in a highly colonial seabird. Proceedings of the Royal Society B Biological Sciences 277: 2355-2360.

Banyard, A.C., Lean, F.Z.X., Robinson, C., Howie, F. et al. 2022. Detection of highly pathogenic avian influenza virus H5N1 clade 2.3.4.4b in great skuas: a species of conservation concern in Great Britain. Viruses 14: 212.

Barbraud, C., Bertrand, A., Bouchon, M., Chaigneau, A. et al. 2018. Density dependence, prey accessibility and prey depletion by fisheries drive Peruvian seabird population dynamics. Ecography 41: 1092-1102.

Barrett, R.T., Strøm, H. and Melnikov, M. 2017. On the polar edge: the status of the northern gannet (*Morus bassanus*) in the Barents Sea in 2015-16. Polar Research 36: 1390384.

Bayes, J.C., Dawson, M.J., Joensen, A.H. and Potts, G.R. 1964. The distribution and numbers of the great skua breeding in the Faeroes in 1961. Dansk Ornitologisk Forenings Tidsskrift 58: 36-41.

Bennett, S., Wanless, S., Harris, M.P., Newell, M.A., Searle, K., Green, J.A. and Daunt, F. 2022. Site-dependent regulation of breeding success: evidence for the buffer effect in the common guillemot, a colonially breeding seabird. Journal of Animal Ecology 91: 752-765.

BirdLife 2022. www.Birdlife.org/news/2022/08/08 accessed 23/09/2022.

Bregnballe, T. and Frederiksen, M. 2021. Conspecific density as a driver of offspring body condition in three cormorant colonies in Denmark. Ardea 109: 593-608.

Buckingham, L., Bogdanova, M.I., Green, J.A., Dunn, R.E. et al. 2022. Interspecific variation in non-breeding aggregation: a multi-colony tracking study of two sympatric seabirds. Marine Ecology Progress Series 684: 181-197.

Caliendo, V., Lewis, N.S., Pohlmann, A., Baillie, S.R. et al. 2022a. Transatlantic spread of highly pathogenic avian influenza H5N1 by wild birds from Europe to North America in 2021. Scientific Reports 12: 11729.

Caliendo, V., Leijten, L., van der Bildt, M.W.G., Poen, M.J. et al. 2022b. Long-term protective effect of serial infections with H5N8 highly pathogenic avian influenza virus in wild ducks. Journal of Virology 96: doi 10.1128/jvi.01233-22.

Camphuysen, C.J. 2022. Beached bird surveys in The Netherlands, autumn 2021 and winter 2021/22. NIOZ Report, Aug 2022. Royal Netherlands Institute for Sea Research, Texel.

Camphuysen, C.K. and Gear, S.C. 2022. Great skuas and northern gannets on Foula, summer 2022 – an unprecedented, H5N1 related massacre. NIOZ Report 2022-02. NIOZ Royal Netherlands Institute for Sea Research, Texel. https://doi.org/10.25850/nioz/7b.b.gd

Camphuysen, C.J., Gear, S.C. and Furness, R.W. 2022. Avian influenza leads to mass mortality of adult great skuas in Foula in summer 2022. Scottish Birds in press.

Chardine, J.W., Rail, J-F. and Wilhelm, S. 2013. Population dynamics of northern gannets in North America, 1984-2009. Journal of Field Ornithology 84: 187-192.

Chen H., Smith, G.J.D., Zhang, S.Y., Qin, K. et al. 2005. H5N1 virus outbreak in migratory waterfowl - A worrying development could help to spread this dangerous virus beyond its stronghold in southeast Asia. Nature 436: 191-192.

Church, G.E., Furness, R.W., Tyler, G., Gilbert, L. and Votier, S.C. 2018. Change in the North Sea ecosystem from the 1970s to the 2010s: great skua diets reflect changing forage fish, seabirds, and fisheries. ICES Journal of Marine Science 76: 925-937.

Convention on Migratory Species 2022. Scientific task force on avian influenza and wild birds statement on: H5N1 highly pathogenic avian influenza in poultry and wild birds: winter of 2021/2022 with focus on mass mortality of wild birds in UK and Israel. 24 January 2022. www.cms.int/sites/default/files/uploads/avian_influenza_0.pdf

Cortes-Hinojosa, G., Broitman, B., Rivadeneira, M. and Luna-Jorquera, G. 2017. Effect of environmental variables and population density on the development of Humboldt penguin (*Spheniscus humboldti*) chicks. Revista Chilena de Ornitologia 23: 55-62.

Coulson, J.C. 1999. Variation in clutch size of the common eider: a study based on 41 breeding seasons on Coquet Island, Northumberland, England. Waterbirds 22: 225-238.

Coulson, J.C., Duncan, N. and Thomas, C. 1982. Changes in the breeding biology of the herring gull (*Larus argentatus*) induced by reduction in the size and density of the colony. Journal of Animal Ecology 51: 739-756.

Cui, P., Shi, J., Wang, C., Zhang, Y. et al. 2022. Global dissemination of H5N1 influenza viruses bearing the clade 2.3.4.4b HA gene and biologic analysis of the ones detected in China. Emerging Microbes and Infections 11: 1693-1704.

Daily Maverick 2022. Deadly avian flu hits endangered penguin colony on Cape Peninsula. https://www.dailymaverick.co.za/article/2022-09-20-deadly-avian-flu-hits-endangered-penguin-colony-on-cape-peninsula/

Danckwerts, D.K., Humeau, L., Pinet, P., McQuaid, C.D. and Le Corre, M. 2021. Extreme philopatry and genetic diversification at unprecedented scales in a seabird. Scientific Reports 11: 6834.

Eda, M., Yamasaki, T., Izumi, H., Tomita, N., Konno, S., Konno, M., Murakami, H. and Sato, F. 2020. Cryptic species in a vulnerable seabird: short-tailed albatross consists of two species. Endangered Species Research 43: 375-386.

Erikstad, K.E., Reiertsen, T.K., Barrett, R.T., Vikebø, F. and Sandvik, H. 2013. Seabird-fish interactions: the fall and rise of a common guillemot *Uria aalge* population. Marine Ecology Progress Series 475: 267-276.

Fay, R., Barbraud, C., Delord, K. and Weimerskirch, H. 2017. Contrasting effects of climate and population density over time and life stages in a long-lived seabird. Functional Ecology 31: 1275-1284.

Finkelstein, M.E., Wolf, S., Goldman, M., Doak, D.F., Sievert, P.R., Balogh, G. and Hasegawa, H. 2010. The anatomy of a (potential) disaster: volcanoes, behavior, and population viability of the short-tailed albatross (*Phoebastria albatrus*). Biological Conservation 143: 321-331.

Fisher, J. and Vevers, H.G. 1943-44. The breeding distribution, history and population of the North Atlantic gannet *Sula bassana*. Journal of Animal Ecology 12: 173-213; 13: 49-62.

Furness, R.W. 1977. Studies on the breeding biology and population dynamics of the great skua (*Catharacta skua* Brünnich). Ph.D. thesis, University of Glasgow.

Furness, R.W. 1981. Colonisation of Foula by gannets. Scottish Birds 11: 211-213.

Furness, R.W. 1987. The Skuas. T. & A.D. Poyser, Calton.

Furness, R.W. 2015. Density dependence in seabirds: great skuas *Stercorarius skua* start to breed at a younger age when conditions are better. Ringing & Migration 30: 43-50.

Furness, R.W. 2022. Recent changes in colony sizes of two seabird species in Scotland are not strongly influenced by Birds Directive status of the colony. Ibis doi: 10.1111/ibi.13127.

Furness, R.W. and Birkhead, T.R. 1984. Seabird colony distributions suggest competition for food supplies during the breeding season. Nature 311: 655-656.

Gardarsson, A. 2019. Icelandic colonies of the northern gannet in 2013-2014. Bliki 33: 69-71.

Gascoigne, J.C. and Lipcius, R.N. 2004. Allee effects driven by predation. Journal of Applied Ecology 41: 801-810.

Gear, S. 2022. Appendix 1 Seabird monitoring on Foula in 2021. pp. 42-44 In Miles, W. and Mellor, M. SOTEAG ornithological monitoring programme – 2021 report. University of St Andrews.

Genovart, M., Oro, D., Juste, J. and Bertorelle, G. 2007. What genetics tells us about the conservation of the critically endangered Balearic shearwater. Biological Conservation 137: 283-293.

Genovart, M., Oro, D. and Tenan, S. 2018. Immature survival, fertility, and density dependence drive global population dynamics in a long-lived species. Ecology 99: 2823-2832.

Gilchrist, H.G. 1999. Declining thick-billed murre *Uria lomvia* colonies experience higher gull predation rates: an intercolony comparison. Biological Conservation 87: 21-29.

Globig A., Staubach, C., Beer, M., Köppen, U. et al. 2009. Epidemiological and ornithological aspects of outbreaks of highly pathogenic avian influenza virus H5N1 of Asian lineage in wild birds in Germany, 2006 and 2007. Transb. Emerg. Dis. 56: 57-72.

Goyert, H.F., Garton, E.O., Drummond, B.A. and Renner, H.M. 2017. Density dependence and changes in the carrying capacity of Alaskan seabird populations. Biological Conservation 209: 178-187.

Goyert, H.F., Garton, E.O. and Poe, A.J. 2018. Effects of climate change and environmental variability on the carrying capacity of Alaskan seabird populations. Auk 135: 975-991.

Grear, J.S., Meyer, M.W., Cooley, J.H., Kuhn, A. et al. 2009. Population growth and demography of common loons in the northern United States. Journal of Wildlife Management 73: 1108-1115.

Hammer, S., Madsen, J.J., Jensen, J-K., Pedersen, K.T., Bloch, D. and Thorup, K. 2014. Færøsk Trækfugleatlas. Faroe University Press, Tórshavn.

Harris, M.P. and Murray, S. 1978. Birds of St Kilda. Institute of Terrestrial Ecology, Banchory.

Hasebe, M., Aotsuka, M., Terasawa, T., Fukuda, Y., Niimura, Y., Watanabe, Y., Watanuki, Y. and Ogi, H. 2012. Status and conservation of the common murre *Uria aalge* breeding on Teuri Island, Hokkaido. Ornithological Science 11: 29-38.

Heubeck, M., Mellor, R.M. and Harvey, P.V. 1997. Changes in the breeding distribution and numbers of kittiwakes *Rissa tridactyla* around Unst, Shetland, and the presumed role of predation by great skuas *Stercorarius skua*. Seabird 19: 12-21.

Horswill, C., O'Brien, S.H. and Robinson, R.A. 2017. Density dependence and marine bird populations: are wind farm assessments precautionary? Journal of Applied Ecology 54: 1406-1414.

Huang Y., G.J. Robertson, D. Ojkic, H. Whitney and A.S. Lang 2014. Diverse inter-continental and host lineage reassortant avian influenza A viruses in pelagic seabirds. Infection, Genetics and Evolution 22: 103-111.

Jhung, M.A. and Nelson, D.I. 2015. Outbreaks of avian influenza A (H5N2), (H5N8), and (H5N1) among birds – United States, December 2014-January 2015. MMWR Morbidity and Mortality Weekly Report 64: 111.

JNCC 2022. Seabird Monitoring Programme Database.
https://app.bto.org/seabirds/public/index.jsp

Jouventin, P., Martinez, J. and Roux, J.P. 1989. Breeding biology and current status of the Amsterdam albatross *Diomedea amsterdamensis*. Ibis 131: 171-182.

Kaplan, B.S. and Webby, R.J. 2013. The avian and mammalian host range of highly pathogenic avian H5N1 influenza. Virus Research 178: 3-11.

Kokubun, N., Emmerson, L., McInnes, J., Wienecke, B. and Southwell, C. 2021. Sea-ice and density-dependent factors affecting foraging habitat and behaviour of Adelie penguins throughout the breeding season. Marine Biology 168: 97.

Kuro-O, M., Yonekawa, H., Saito, S., Eda, M., Higuchi, H., Koike, H. and Hasegawa, H. 2010. Unexpectedly high genetic diversity of mtDNA control region through severe bottleneck in vulnerable albatross *Phoebastria albatrus*. Conservation Genetics 11: 127-137.

Lamb, J.S., Stage, Y.G. and Jodice, P.G.R. 2017. Influence of density-dependent competition on foraging and migratory behavior of a subtropical colonial seabird. Ecology and Evolution 7: 6469-6481.

Lang, A.S., Lebarbenchon, C., Ramey, A.M., Robertson, G.J. and Waldenström, J. 2016. Assessing the role of seabirds in the ecology of influenza A viruses. Avian Diseases 60: 378-386.

Lawrence, H.A., Taylor G.A., Millar, C.D. and Lambert, D.M. 2008. High mitochondrial and nuclear genetic diversity in one of the world's most endangered seabirds, the Chatham Island taiko (*Pterodroma magentae*). Conservation Genetics 9: 1293-1301.

Lycett, S.J., Bodewes, R., Pohlmann, A., Banks, J. et al. 2016. Role for migratory wild birds in the global spread of avian influenza H5N8. Science 354: 213-217.

te Marvelde, L., Meininger, P.L., Flamant, R. and Dingemanse, N.J. 2009. Age-specific density-dependent survival in Mediterranean gulls *Larus melanocephalus*. Ardea 97: 305-312.

McKnight, A., Blomberg, E.J., Irons, D.B., Loftin, C.S. and McKinney, S.T. 2019. Survival and recruitment dynamics of black-legged kittiwakes *Rissa tridactyla* at an Alaskan colony. Marine Ornithology 47: 209-222.

Miles, W., Mellor, M., Clark, J., Reay, S., Pennington, M., Tyler, G., Kelly, K. and Gear, S. 2022. Seabird breeding season summary. Shetland Bird Club Newsletter No. 196.

Miller, J.A.O., Furness, R.W., Trinder, M. and Matthiopoulos, J. 2019. The sensitivity of seabird populations to density-dependence, environmental stochasticity and anthropogenic mortality. Journal of Applied Ecology 56: 2118-2130.

Minias, P., Wlodarczyk, R. and Janiszewski, T. 2015. Opposing selection pressures may act on the colony size in a waterbird species. Evolutionary Ecology 29: 283-297.

Mitchell, P.I., Newton, S.F., Ratcliffe, N. and Dunn, T.E. 2004. Seabird Populations of Britain and Ireland. T. & A.D. Poyser, London.

Munilla, I., Genovart, M., Paiva, V.H. and Velando, A. 2016. Colony foundation in an oceanic seabird. PLoS ONE 11: e0147222.

Murray, S., Harris, M.P. and Wanless, S. 2015. The status of the gannet in Scotland in 2013-14. Scottish Birds 35: 3-18.

Nager, R.G. and O'Hanlon, N.J. 2016. Changing numbers of three gull species in the British Isles. Waterbirds 39: 15-28.

National Geographic 2022. The UK's largest avian flu outbreak has left millions of birds dead – and scientists extremely concerned | National Geographic

Natural England 2022. Highly Pathogenic Avian Influenza (HPAI) outbreak in seabirds and Natural England advice on impact assessment (specifically relating to offshore wind) September 2022. Natural England, Peterborough.

Nelson, J.B. 1978. The Sulidae: gannets and boobies. Oxford University Press, Oxford.

Oro, D. and Furness, R.W. 2002. Influences of food availability and predation on survival of kittiwakes. Ecology 83: 2516-2528.

Oro, D., Martinez-Abrain, A., Paracuellos, M., Nevado, J.C. and Genovart, M. 2006. Influence of density dependence on predator-prey seabird interactions at large spatio-temporal scales. Proceedings of the Royal Society B 273: 379-383.

Oro, D., Becares, J., Bartumeus, F. and Arcos, J.M. 2021. High frequency of prospecting for informed dispersal and colonisation in a social species at large spatial scale. Oecologia 197: 395-409.

Pacoureau, N., Authier, M., Delord, K. and Barbraud, C. 2019. Population response on an apex Antarctic consumer to its prey and climate fluctuations. Oecologia 189: 279-291.

Patterson, A., Gilchrist, H.G., Benjaminsen, S., Bolton, M. et al. 2022. Foraging range scales with colony size in high-latitude seabirds. Current Biology 32: 3800-3807.

Payo-Payo, A., Genovart, M., Bertolero, A., Pradel, R. and Oro, D. 2016. Consecutive cohort effects driven by density-dependence and climate influence early-life survival in a long-lived bird. Proceedings of the Royal Society B – Biological Sciences 283: 20153042.

Pearce-Higgins, J. and Toms, M. 2022. Tragedy of the colonies. BTO News 344: 12-15.

Pennington, M., Osborn, K., Harvey, P., Riddington, R., Okill, D., Ellis, P. and Heubeck, M. 2004. The Birds of Shetland. Christopher Helm, London.

Perry, R. 1948. Shetland Sanctuary. Faber & Faber, London.

Philip, E. and Tyler, G. 2022. Weathering the storm: a policy response. [Surveillance and monitoring responses to Highly Pathogenic Avian Influenza, a workshop at Cork Seabird Conference (2022) - YouTube]

Phillips, R.A. and Furness, R.W. 1998. The influence of territory density on the vulnerability of Arctic skuas *Stercorarius parasiticus* to predation. Biological Conservation 86: 21-31.

Potts, G.R., Coulson, J.C. and Deans, I.R. 1980. Population dynamics and breeding success of the shag, *Phalacrocorax aristotelis*, on the Farne Islands, Northumberland. Journal of Animal Ecology 49: 465-484.

Pöysä, H. and Pöysä, S. 2002. Nest-site limitation and density dependence of reproductive output in the common goldeneye *Bucephala clangula*: implications for the management of cavity-nesting birds. Journal of Applied Ecology 39: 502-510.

Radio Canada 2022. https://ici.radio-canada.ca/nouvelle/1899344 and https://ici.radio-canada.ca/nouvelle/1915297

Ramey A.M., A.B. Reeves, B.J. Lagassé, V. Patil, L.E. Hubbard, D.W. Kolpin, R.B. McCleskey, D.A. Repert, D.E. Stallknecht and R.L. Poulson 2022. Evidence for interannual persistence of infectious influenza A viruses in Alaska wetlands. Science of the Total Environment 803: 150078.

Real, E., Oro, D., Martinez-Abrain, A., Manuel Igual, J., Bertolero, A., Bosch, M. and Tavecchia, G. 2017. Predictable anthropogenic food subsidies, density-dependence and socio-economic factors influence breeding investment in a generalist seabird. Journal of Avian Biology 48: 1462-1470.

Rijks, J.M., Leopold, M.F., Kühn, S., in 't Veld, R., Schenk, F., Brennunkmeijer, A., Lilipaly, S.J., Ballmann, M.Z., Kelder, L., de Jong, J.W., Courtens, W., Slaterus, R., Kleyheeg, E., Vreman, S., Kik, M.J.L., Gröne, A., Fouchier, R.A.M., Engelsma, M., de Jong, M.C.M., Kuiken, T. and Beerens, N. 2022. Mass mortality caused by highly pathogenic influenza A (H5N1) virus in Sandwich terns, the Netherlands, 2022. Emerging Infectious Diseases 28: 2538-2542.

Roche B., C. Lebarbenchon, M. Gauthier-Clerc, C-M Chang, F. Thomas, F. Renaud, S. van der Werf and J-F. Guégan 2009. Water-borne transmission drives avian influenza dynamics in wild birds: The case of the 2005-2006 epidemics in the Camargue area. Infection, Genetics & Evolution 9: 800-805.

RSPB 2022. How together we can protect wild birds from Avian Flu. https://rspb.org.uk/birdflu accessed 23/09/2022.

Sato, F. 2009. Increase in pairs of the short-tailed albatross *Diomedea albatrus* at an artificial breeding ground. Journal of the Yamashina Institute for Ornithology 40: 139-143.

Schippers, P., Stienen, E.W.M., Schotman, A.G.M., Snep, R.P.H. and Slim, P.A. 2011. The consequences of being colonial: Allee effects in metapopulations of seabirds. Ecological Modelling 222: 3061-3070.

Serrano, D., Oro, D., Ursua, E. and Tella, J.L. 2005. Colony size selection determines adult survival and dispersal preferences: Allee effects in a colonial bird. American Naturalist 166: E22-E31.

Sonnberg, S., Webby, R.J. and Webster, R.G. 2013. Natural history of highly pathogenic avian influenza H5N1. Virus Research 178: 63-77.

Southwell, C. and Emmerson, L. 2020. Density dependence forces divergent population growth rates and alters occupancy patterns of a central place foraging Antarctic seabird. Ecology and Evolution 10: 2339-2351.

Southwell, C., Wotherspoon, S. and Emmerson, L. 2021. Emerging evidence of resource limitation in an Antarctic seabird metapopulation after 6 decades of sustained population growth. Oecologia 196: 693-705.

Vader, W., Barrett, R.T., Erikstad, K.E. and Strann, K.B. 1990. Differential responses of common and thick-billed murres to a crash in the capelin stock in the southern Barents Sea. Studies in Avian Biology 14: 175-180.

Votier, S.C., Furness, R.W., Bearhop, S., Crane, J.E. et al. 2004. Changes in fisheries discard rates and seabird communities. Nature 427: 727-730.

Votier, S.C., Heubeck, M. and Furness, R.W. 2008. Using inter-colony variation in demographic parameters to assess the impact of skua predation on seabird populations. Ibis 150: 45-53.

Votier, S.C., Hatchwell, B.J., Mears, M. and Birkhead, T.R. 2009. Changes in the timing of egg-laying of a colonial seabird in relation to population size and environmental conditions. Marine Ecology Progress Series 393: 225-233.

Wakefield, E.D., Owen, E., Baer, J., Carroll, M.J. et al. 2017. Breeding density, fine-scale tracking, and large-scale modelling reveal the regional distribution of four seabird species. Ecological Applications 27: 2074-2091.

Weber, S.B., Richardson, A.J., Brown, J., Bolton, M. et al. 2021. Direct evidence of a prey depletion "halo" surrounding a pelagic predator colony. Proceedings of the National Academy of Sciences of the United States of America 118: e2101325118.

WeimerCheckedskirch, H., Brothers, N. and Jouventin, P. 1997. Population dynamics of wandering albatross *Diomedea exulans* and Amsterdam albatross *D. amsterdamensis* in the Indian Ocean and their relationships with long-line fisheries: conservation implications. Biological Conservation 79: 257-270.

Welch, A.J., Wiley, A.E., James, H.F., Ostrom, P.H., Stafford, T.W. and Fleischer, R.C. 2012. Ancient DNA reveals genetic stability despite demographic decline: 3,000 years of population history in the endemic Hawaiian petrel. Molecular Biology and Evolution 29: 3729-3740.

Werner, A.C., Paiva, V.H. and Ramos, J.A. 2014. On the "real estate market": individual quality and the foraging ecology of male Cory's shearwaters. Auk 131: 265-274.

WHO 2022. Cumulative number of confirmed human cases for avian influenza A (H5N1) reported to WHO, 2003-2022. www.who.int/publications_2022_june_tableh5n1.pdf

Wille, M., Huang, Y., Roberston, G.J., Ryan, P. et al. 2014. Evaluation of seabirds in Newfoundland and Labrador, Canada, as hosts of influenza A viruses. Journal of Wildlife Diseases 50: 98-103.