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REVIEW

Current understanding of how climate change affects seabirds varies between regions and species in the North-East Atlantic

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ABSTRACT: Climate change is regarded as a major threat to seabird populations globally. While the impacts on certain species are well-studied, the majority remain understudied, which may limit our understanding of the key mechanisms linking climate change to population dynamics. This information is important to identify vulnerable species and inform potential conservation responses. To address this gap, we reviewed literature on the impacts of climate change on the demography of 25 seabird species breeding in the UK and Republic of Ireland from relevant studies conducted within the wider North-East Atlantic. We found regional and species-specific variations in research effort, with the North Sea being the most studied area. The most frequently studied species were common guillemot *Uria aalge* (n = 35), black-legged kittiwake *Rissa tridactyla* (n = 29), and European shag *Gulosus aristotelis* (n = 25). Breeding productivity and population abundance were the primary demographic parameters investigated. The North Atlantic Oscillation and sea surface temperature were commonly used to describe climate influences, often linked to bottom-up mechanisms affecting demography through changes in prey availability. Breeding productivity was the most monitored demographic rate across species; this may lead to important mechanisms affecting other demographic rates, such as survival, being overlooked. Regional and species-specific disparities in research could bias the identification of key mechanisms. Despite these uncertainties, current literature highlights the importance of climate impacts through the food chain and severe storm events affecting seabirds. In response, climate change adaptation should prioritise management of fish stocks near breeding colonies and coastal management to protect vulnerable colonies from storm events.

KEY WORDS: Seabirds · Climate change · Review · Monitoring · Demographic consequences · Bias

1. INTRODUCTION

Climate change is impacting natural systems across the globe, leading to detectable changes in the demographic rates of many species (Scheffers et al. 2016). Seabirds appear particularly vulnerable (Pearce-Higgins & Green 2014), including in the North Atlantic, where many species are projected to suffer sus-

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*Corresponding author: daniel.johnston@bto.org tained population declines during the course of this century (Johnston et al. 2013, Russell et al. 2015, Davies et al. 2023, Häkkinen et al. 2023). A number of long-term studies have established that seabird populations respond to climate change through changes in abundance, breeding productivity, survival rates, and phenology (Harris et al. 2006, Lauria et al. 2012, Sandvik et al. 2012). Demographic responses may be related to climate variables such as sea surface temperature (SST) and the North Atlantic Oscillation (NAO) Index (see Table 2 for definition) (Frederiksen et al. 2004a, Burthe et al. 2012, Dias et al. 2019, Mitchell et al. 2020), but the mechanisms underlying these relationships are often unclear. To inform effective conservation action, it is important to identify the main mechanisms by which climate change may affect seabird populations. However, to date, studies on climate-driven mechanisms have primarily focussed on a limited number of species and populations, often within a restricted geographic range (Pearce-Higgins & Green 2014).

1.1. Climate-driven mechanisms

Indirect mechanisms linking climate to seabird demography may arise through bottom-up impacts on the abundance, quality, or distribution of prey, which are influenced in turn by changes in primary productivity and oceanographic features (Frederiksen et al. 2006). The availability and abundance of prey can be affected by the spatial distribution of phytoplankton (Bedford et al. 2020) or the strength and timing of the spring phytoplankton bloom, an event closely tied to water-column stratification and SST (Scott et al. 2006). Variation in the timing of prey species migrations may also lead to changes in their temporal availability to seabirds (Røttingen 1990). Alignment in the timing of the chick-rearing period and the emergence and peak lipid content of prey is important for the attainment of high breeding productivity in some seabirds (Burthe et al. 2012, Pearce-Higgins & Green 2014). Changes in the timing of breeding may lead to a mismatch between the energetic demands of chicks and the quality and abundance of prey (Samplonius et al. 2021); however, multi-species shifts in the breeding timing of seabirds are hard to discern (Keogan et al. 2018). Prey abundance during the winter is likely to influence body condition and survival of both adult and immature seabirds, with possible carryover effects on adults in the subsequent breeding season with implications for reproductive output (Salton et al. 2015).

Seabird populations may experience multiple direct and indirect effects of climate change simultaneously (Oro 2014). Furthermore, the impacts of climate change may be masked by mortality linked to other anthropogenic threats such as oil spills (Votier et al. 2005) and plastic ingestion (O'Hanlon et al. 2017) or diseases such as avian influenza (Blagodatski et al. 2021). Long-term fisheries practices may also contribute to negative demographic rates of seabirds, through prey depletion (Furness & Tasker 2000, Frederiksen et al. 2004b), changes in discard rates (Church et al. 2019), or by-catch (Žydelis et al. 2009). Therefore, the effects of climate change on a population may be hard to disentangle from other simultaneously occurring impacts.

1.2. Vulnerability to climate change

Although it is possible to identify a wide range of potential mechanisms by which climate change may affect seabirds, the extent that species are impacted by changes in their environment is largely determined by their physiology (Whitehead et al. 2022), foraging ecology (Frederiksen et al. 2007), and breeding behaviour (Moe et al. 2009). Surface-feeding species may be more vulnerable to changes in food availability or distribution in the surface waters, due to their inability to exploit the greater depths used by diving species (Furness & Tasker 2000), while seabirds with more flexible diets can adjust to changes in their food supply (Howells et al. 2018). High winds and wave heights may also disproportionately impair the ability of pursuit plunging species to forage (Birkhead 1976, Taylor 1983, Morley et al. 2016).

1.3. Detection of climate-change-mediated impacts on seabirds

Conspicuous nesting habits by many cliff- and ground-nesting seabirds often allow for intensive monitoring of seabird abundance, breeding productivity, recruitment, phenology, or survival (Walsh et al. 1995). The temporal scale required to detect species-level impacts will vary between demographic rates (Oro 2014). For many species, breeding productivity is often readily monitored, providing a relatively immediate indication of the environmental conditions preceding or occurring during the breeding season (Furness & Camphuysen 1997, Furness & Tasker 2000). In contrast, trends in seabird abundance require decades of monitoring for a measurable impact to be observed due to the longevity and high adult survival rates of seabirds which buffer populations from short-term deleterious environmental conditions (Heath et al. 2009), unless catastrophic mortalities result. Unlike for productivity, decades of mark—recapture/resight effort are required to detect an impact of climate on survival (Oro 2014).

1.4. Aims and objectives

The effects of climate-mediated change on seabird populations have previously been reviewed (Heath et al. 2009, Sydeman et al. 2012, Daunt & Mitchell 2013, Oro 2014, Pearce-Higgins & Green 2014, Daunt et al. 2017, Mitchell et al. 2020). However, these reviews have not robustly quantified the key climate mechanisms underpinning seabird population responses. We aim to highlight the weight of evidence for different mechanisms through which climate change has impacted all seabird species breeding in the UK and Republic of Ireland (hereafter the 'key seabird species'), by using studies carried out in the North-East Atlantic. To address this aim, we therefore (1) identify through the literature the climate variables impacting the key seabird species; (2) classify and quantify mechanism parameters by which the climate variables impact seabirds; and (3) examine the extent of knowledge of the demographic responses to these mechanism parameters between species and species groups.

2. METHODS

2.1. Literature search

A structured literature review was performed, through a standardised internet search for the years 1970—2022, using Web of Science (webofscience.com), supplemented by Google Scholar (scholar.google.com). Search terms used were divided by species (indicated by common name and scientific name/s) and key words ('climate change', 'sea-surface temperature', 'precipitation', 'adverse weather', 'extreme weather', 'NAO', 'stratification', 'global warming', and 'ocean warming'). Where multiple common or scientific names were applicable to a single species, these were also included within the search terms. An example search would comprise a series of terms queried as: ('European Shag' OR 'Gulosus aristotelis' OR 'Phalacrocorax aristotelis') AND ('climate change' OR 'sea-surface temperature' OR 'precipitation' OR 'adverse weather' OR 'extreme weather' OR 'NAO' OR 'stratification' OR 'global warming' OR 'ocean warming').

Applying this approach, 736 studies were compiled across the 25 species through Web of Science, of which 187 studies pertained to multiple species. Relevant studies were refined based on their titles and abstracts, selecting studies which considered the influence of climate on the demography of a target seabird species. Additionally, studies were restricted to those conducted within the North-East Atlantic, confined to the OSPAR region, a region defined by the Convention for the Protection of the Marine Environment of the North-East Atlantic (OSPAR), and the Mediterranean Sea. A review of abstracts indicated that 72 papers were relevant. A further literature search using Google Scholar, citations, and review papers increased the number of relevant studies to 142 (Table 1). Of the reviewed papers, only studies which explicitly examined a climate variable in relation to the demography of a species were considered; this refined the number of applicable studies to 112 (Table 1).

2.2. Mechanisms

From each study, we extracted the study species, location, and duration. Study locations were grouped according to their proximity to regional seas as defined by the European Environment Agency (www.eea.europa.eu/data-and-maps/figures/regional-ses-surrounding-europe-1). Study durations were classified as either short-term (≤5 yr) or long-term (>5 yr). To examine the response to climate by study species of similar life history, species were categorised by their foraging ecology as defined by the OSPAR Commission (2016): surface, midwater, or benthic diving species.

Variables examined in each study were categorised into 5 parameter groups (defined in Table 2): 'climate variable'; 'biotic' and 'behavioural/physiological' mechanistic steps; and 'individual' and 'demographic' level impacts. Using these parameters, we described the responses of individual species and locations to climate variables. However, studies may contain analyses examining multiple study locations, species, climate variables, and demographic impacts. To account for this, we categorised a suite of analysis by the species, study sites, and climate variables examined (Fig. 1).

Table 1. Seabird species reviewed and the number of identified studies relevant to the North-East Atlantic study area. 'Studies incorporating climate' are the number of studies which explicitly examined a climate variable in relation to demography. The number of studies defined as short (≤5 yr) and long (>5 yr) term are displayed per species. In total, 142 studies are included, of which 24 considered multiple species. Species codes are used in Figs. 3 & 4

Foraging group	Common name	Binomial	Species code	Study length		Studies reviewed (n)	Studies incorporating climate (n)
				Short	Long		
Benthic	Black guillemot	*Cepphus grylle*	TY	1	3	4	4
	European shag	*Gulosus aristotelis*	SA	7	18	25	24
	Great cormorant	*Phalacrocorax carbo*	CA	1	5	6	5
Midwater	Atlantic puffin	*Fratercula artica*	PU	0	15	15	14
	Common guillemot	*Uria aalge*	GU	6	29	35	30
	Razorbill	*Alca torda*	RA	2	10	12	12
	Northern gannet	*Morus bassanus*	GX	1	4	5	5
Surface	Arctic skua	*Stercorarius parasiticus*	AC	1	3	4	0
	Arctic tern	*Sterna paradisaea*	AE	1	7	8	8
	Black-legged kittiwake	*Rissa tridactyla*	KI	3	26	29	21
	Black-headed gull	*Chroicocephalus ridibundus*	BH	3	7	10	9
	Common gull	*Larus canus*	GM	2	6	8	6
	Common tern	*Sterna hirundo*	CN	5	6	11	11
	Great black-backed gull	*Larus marinus*	GB	0	3	3	2
	Great skua	*Stercorarius skua*	NX	4	1	5	2
	Herring gull	*Larus argentatus*	HG	0	5	5	3
	Leach's petrel	*Oceanodroma leucorhoa*	TL	2	0	2	0
	Lesser black-backed gull	*Larus fuscus*	LB	1	5	6	5
	Little tern	*Sterna albifrons*	AF	0	5	5	5
	Manx shearwater	*Puffinus puffinus*	MX	2	1	3	3
	Mediterranean gull	*Ichthyaetus melanocephalus*	MU	0	2	2	1
	Northern fulmar	*Fulmaris glacialis*	F.	1	8	9	8
	Roseate tern	*Sterna dougallii*	RS	0	1	1	1
	Sandwich tern	*Thalasseus sandivcensis*	TE	2	5	7	7
	Storm petrel	*Hydrobates pelagicus*	TM	2	3	5	2

Parameters extracted for each individual study, or component of a suite of analysis, may be linked by a sequence of influence, composed of mechanistic steps. A complete mechanism contained: a climate variable (e.g. SST); a biotic parameter (e.g. a change to prey abundance); a behavioural/physiological step (e.g. a change in foraging ability); the observed impact on an individual (e.g. reduction in chick provisioning); the overall demographic impact experienced by a population (e.g. decline in breeding productivity) (Fig. 1). The frequency at which a parameter was studied was used to quantify the evidence supporting a potential mechanism.

We recorded whether the statistical analysis within a study indicated that a climate variable, mediated via a mechanism, exhibited a statistically significant impact on a demographic parameter. The direction of each result was assessed as being positive, negative, or mixed/no effect. In cases where multi-model inference was used within a study, a significant effect was signified by a climate covariate being contained within the most parsimonious model(s).

2.3. Analysis

To quantify the typical response of a species to individual parameters identified in the literature, we developed a 'relative response' index. This index reflects both the magnitude and direction (positive or negative) of the species' responses. The relative response was calculated by determining the net significant response, which is the difference between the total weighted positive significant responses and the total weighted negative significant responses. This approach allows the index to capture the extent and direction or response by a species to a parameter.

The contribution of each study to the index was weighted by its spatial and temporal extent. Specifically, the number of study sites was categorised on a 3-point scale: '1–10 sites' = 1, '11–20 sites' = 2, and '20+ sites' = 3. The duration of the study was categorised into 2 points: '≤5 yr' = 1 and '>5 yr' = 2. By integrating these weights, the relative response index provides a measure reflecting the typical direction and magnitude of a species' response to specific parameters, accounting for spatial and temporal extent of the studies reviewed:

Table 2. Definitions of climate variables, environmental covariates, and mechanism parameters identified within the reviewed literature

Parameter group	Parameter	Definition
Climate variable	Air temperature	Measure of the intensity of heat in the air
	Extra-tropical cyclones	Storm systems emerging from mid (30°) to high (90°) latitudes outside of the tropics
	North Atlantic Oscillation Index	Index summarizing the air pressure differential between Iceland and the Azores
	Northern Hemisphere Temperature Anomaly	Anomalous temperatures within the Northern Hemisphere
	Oceanographic conditions	Bathymetry, stratification, turbulence, and vertical currents
	Potential energy anomaly	Measure of the strength of stratification within the ocean water column
	Precipitation	Amount of rainfall recorded within a given period
	Sea level	Height of the sea in relation to high tide water mark
	Sea surface temperature	Measure of water temperature close to the sea surface
	Snow cover	Extent of snow coverage on the ground
	Southern Oscillation Index	Standardised index of sea level pressure differences between Tahiti and Darwin, Australia
	Subpolar Gyre Index	Index of sea surface height in the North Atlantic Ocean
	Temperature Anomaly Index	Integrated index combining ocean and land surface air temperature into an anomaly
	Wind conditions	Wind speed and direction
Biotic	Marine invertebrates (phenology/abundance/composition)	Timing, population size, and species composition of plankton blooms
	Prey availability	Accessibility of a prey population to a foraging seabird
	Terrestrial invertebrates (phenology)	Timing of terrestrial invertebrate emergence in spring
	Prey abundance	Population size of prey species
Behavioural/ physiological	Chick provisioning	Frequency, quality, and quantity of prey fed to chicks
	Foraging ability	Ability of an individual to capture prey; includes foraging efficiency
	Nest attendance	Frequency and length of incubation or chick-guarding bouts at the nest
	Physiological stress	Strain to normal functioning experienced by an individual; includes instances of skipped breeding, disorientation, temperature stress
Individual	Adult condition	Physical condition of an individual of breeding age, usually an index of body mass
	Breeding date/duration	Timing of breeding: laying dates; duration of laying; hatching dates
	Breeding habitat	Quality and accessibility of suitable breeding habitat
	Chick/egg condition	Physical condition of chicks or eggs: chick/egg size and weight; clutch size; chick survival
	Diet composition	Composition of prey species within an individual's diet
	Dispersal	Distance of a breeding individual from its previous breeding site or natal site
	Fledgling sex ratio	Ratio of male to female offspring
	Population phenotype occurrence	Frequency of phenotypic traits within a population
	Timing of migration	Date on which an individual begins post-breeding or pre-breeding migration
Demographic	Adult survival rate	Proportion of adult birds which survive each year
	Breeding abundance	Number of breeding individuals forming a population
	Breeding productivity	Number of successful offspring produced by a breeding pair
	Breeding range	Spatial extent within which a population may successfully breed
	Recruitment	Rate at which immature individuals join a breeding population
	Winter range	Extent of the spatial range reached by a migratory population in winter
	Wintering abundance	Extent of the population size of a migratory or resident population in winter

$$\text{Relative response} = \left(\frac{\sum_{pos=1}^{p} (N_{pos} \times L_{pos}) - \sum_{neg=1}^{n} (N_{neg} \times L_{neg})}{\sum_{ind=1}^{t} (N_{ind} \times L_{ind})} \right) \qquad (1)$$

where p: total number of studies citing a significant positive response for an individual species and parameter; n: total number of studies citing a significant negative response for an individual species and parameter; t: total number of studies considered for an individual species and parameter; S: overall number of studies considered in the analysis; N_{pos}: number of study sites within study *pos* citing a significant positive response; L_{pos}: length of study *pos* citing a significant positive response; N_{neg}: number of study sites within study *neg* citing a significant negative response; L_{neg}: length of study *neg* citing a significant negative response; N_{ind}: total number of study sites within study *ind* (significant or non-significant response); and L_{ind}: total length of study *ind* (significant or non-significant response).

All analyses were conducted using R (version 4.2.2; R Development Core Team 2022). The relative responses of each species to individual mechanistic parameters were visualised using a heat map with a colour gradient to represent the magnitude of each response (see Fig. 4).

3. RESULTS

3.1. Summary of the available literature

The number of available studies varied spatially throughout the North-East Atlantic, with the highest concentration in the North Sea (n = 63), followed by the Celtic Seas (n = 19), Barents Sea (n = 14), Norwegian Sea (n = 12), and Baltic Sea (n = 11) (Fig. 2). The Isle of May, within the North Sea, was the most researched location, with 29 studies. The number of studies also varied greatly between species. The 3 most commonly studied species were European shag *Gulosus aristotelis* (hereafter referred to as 'shag'), common guillemot *Uria aalge* (hereafter 'guillemot'), and black-legged kittiwake *Rissa tridactyla* (hereafter 'kittiwake'; Table 1 contains the species codes used in Figs. 3 & 4), which together contributed 40% of the species/study combinations (Table 2). Although most seabird species examined are surface foragers (18 species), relatively few of these species were well-researched (average 7 studies per species), while a higher proportion of benthic- (11 studies per species) or mid-water-foraging (16 studies per species) species were well-researched. Across most species, studies reliant on long-term (>5 yr) data sets (n = 178) significantly outnumber short-term (≤5 yr) studies (n = 47). Widely studied species such as kittiwake, shag, guillemot, razorbill and Atlantic puffin (hereafter 'puffin') were most frequently subject to long-term studies. Short-term studies were primarily associated with shag, great skua, and common tern (Table 1).

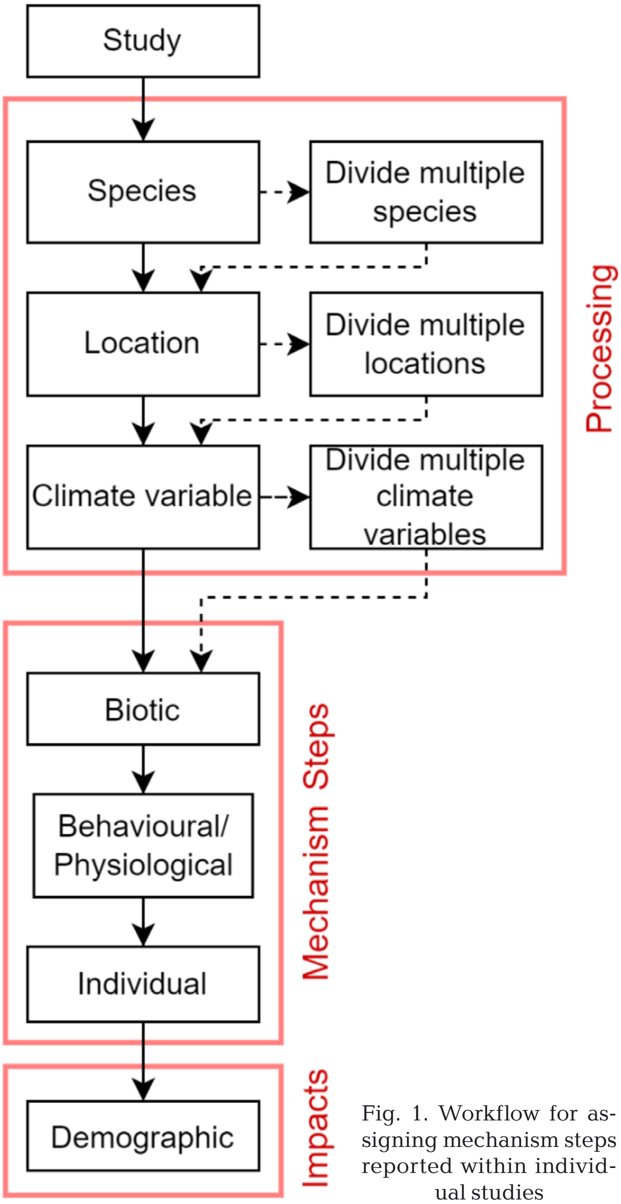

Fig. 1. Workflow for assigning mechanism steps reported within individual studies

A wide range of mechanism parameters were investigated across study species; however, research was found to focus on a few key mechanism parameters (Fig. 1, Table 2). NAO and SST were the most frequently investigated climate parameters, particularly for guillemot, puffin, shag, kittiwake, and razorbill. NAO was relatively well studied in relation to fulmar (n = 7) and Arctic tern (n = 5). Air temperature (n = 29, across 13 species), precipitation (n = 16, across 8 species), and wind conditions (n = 37, across 13 species) were investigated across multiple different species. Studies examining prey abundance and availability were particularly well represented for kittiwake, guillemot, puffin, and shag.

The most commonly studied behavioural or physiological response to climate was chick provisioning (n = 35, across 7 species). Physiological responses to climate were examined in a small number of studies across 12 species. Breeding date/duration was the most examined individual response to climate (n = 80, across 16 species), most numerously examined in shag (n = 19) and guillemot (n = 13) (Fig. 3). Chick and egg condition was another commonly researched individual response to climate (n = 19). Adult con-

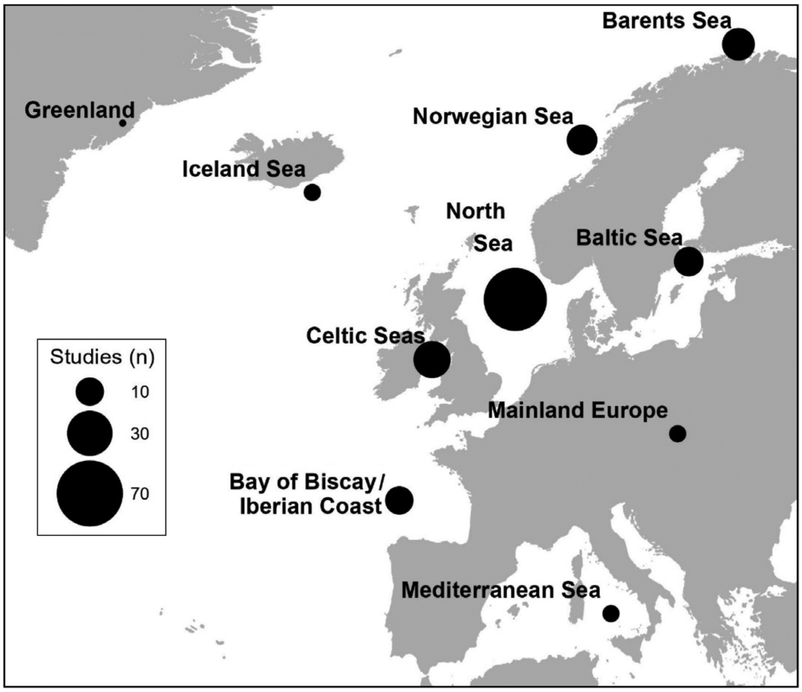

Fig. 2. Spatial distribution and number of studies reviewed. Study locations are grouped by regional seas as defined by the European Environment Agency (www.eea.europa.eu/data-and-maps/figures/regional-ses-surrounding-europe-1)

dition was studied primarily in kittiwake (n = 5). The most studied demographic parameters were adult survival (n = 29, across 8 species), breeding productivity (n = 83, across 17 species), and breeding abundance (n = 53, across 19 species). The response of productivity to climate was particularly well-studied in kittiwake (n = 18), shag (n = 13), puffin (n = 9), and guillemot (n = 12). Winter abundance and range were rarely studied and are primarily examined only in gull species.

3.2. Identifying the most important mechanisms of climate impact on seabirds

Negative relative responses to NAO were found for fulmar, guillemot, and Arctic tern (Fig. 4). Strong negative responses to SST were found for shag and kittiwake. Wind conditions alone were influential on shag, kittiwake, guillemot, and razorbill. Wind conditions alongside precipitation and sea level, which are potentially related to storminess, were particularly important for shag, and to a lesser extent, Arctic and common terns. Air temperature elicited a positive response in black-headed and common gulls.

Prey availability and abundance were the most frequently studied biotic parameters, with responses exhibited by guillemot, kittiwake, puffin, and shag (Fig. 4). Negative response to the impact of bottom-up marine invertebrate processes preceding prey abundance and availability were primarily attributed to kittiwake. This may have been linked to behavioural or physiological responses by kittiwake exhibited through foraging ability and chick provisioning. Common gull was positively associated with changes in terrestrial invertebrates impacting prey availability.

Several species experienced physiological stress, including shag, razorbill, black-headed gull, common tern, and Manx shearwater (Fig. 4). Physiological stress was found to manifest in various behavioural differences, including nest attendance in great skua and foraging ability and chick provisioning in fulmar and kittiwake. Individual-level impacts varied between species; however, negative responses were often exhibited through adult and chick/egg condition. The response by species to breeding date and duration varied, with positive responses exhibited in black guillemot, cormorant, and black-headed and common gulls, while negative responses were exhibited in shag, razorbill, kittiwake, and Sandwich tern.

Demographic rates that displayed the greatest response across species included adult survival rate and breeding productivity, particularly in kittiwake, guillemot, puffin, and shag (Fig. 4). Breeding abundance was frequently studied across species, but its response varied, in contrast to primarily negative response to SST observed in breeding productivity for most species.

4. DISCUSSION

We map for the first time the distribution of literature on climate change impacts on seabirds in the North-East Atlantic, a group highly vulnerable to climate change (Johnston et al. 2013, Davies et al. 2023). There are significant gaps in the literature, as only 6 species have been the focus of more than 10 studies, and of these, only 3 species have been

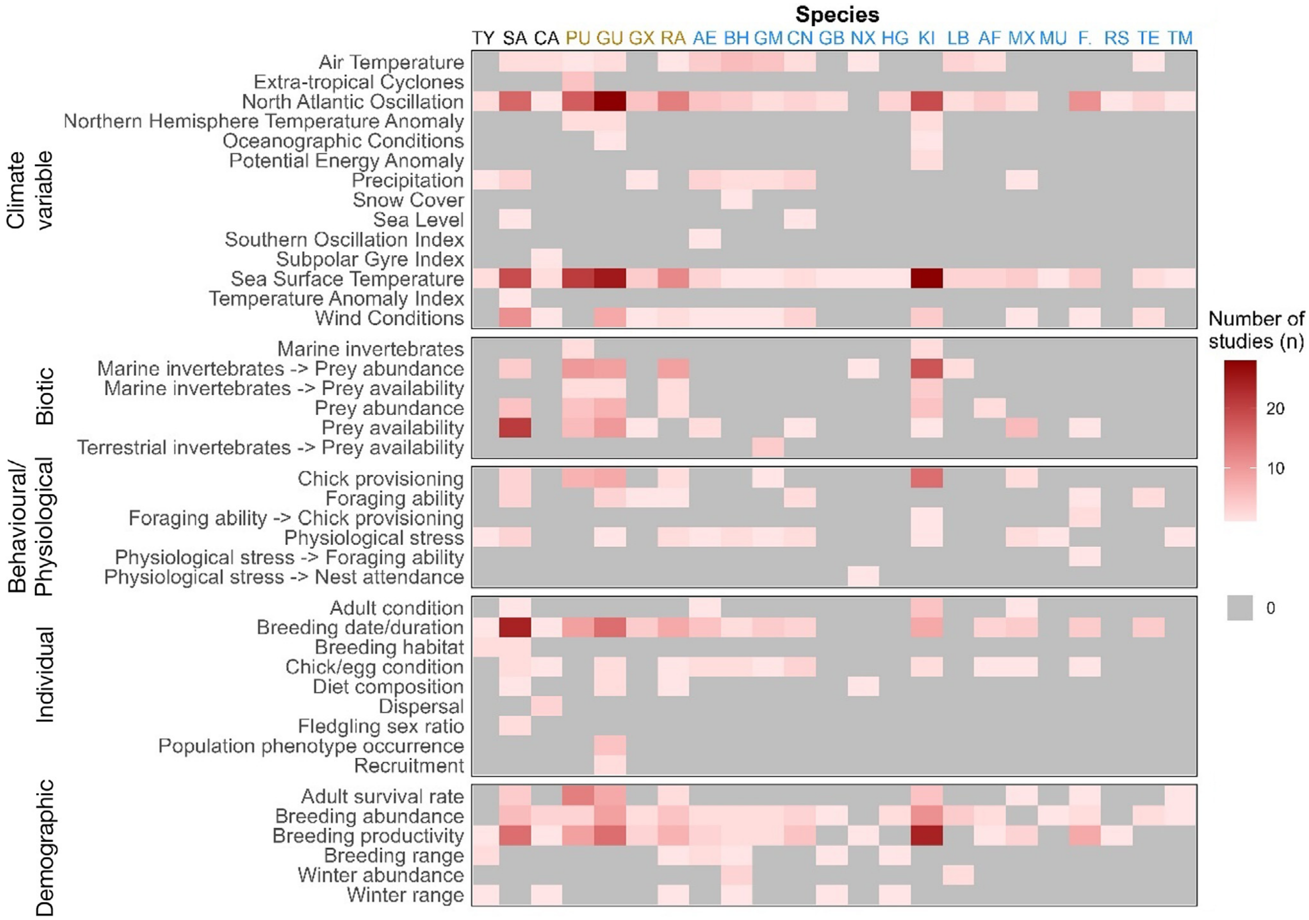

Fig. 3. Number of studies in relation to parameter and species, categorised by parameter groups including climate variables; a biotic covariate; a behavioural or physiological response; an individual-level response; and a demographic-level impact. Cells are shown in shades of red based on the number of studies (n). Species are coloured by foraging group: benthic foraging (black), midwater foraging (yellow), and surface foraging (blue). Species codes and climate variable definitions are given in Table 1

examined in more than 20 studies. The majority of studies were concentrated in and around the North Sea and therefore may not be representative of oceanic conditions in other regional seas. Despite strong evidence of bottom-up processes impacting the breeding productivity and survival rate of guillemot, puffin, kittiwake, and shag, there were differences in the amount and form of evidence on behavioural/physiological and individual mechanisms, and much weaker evidence of mechanisms and impacts for other seabird species. Although there is a relatively large volume of literature on the impacts of climate change on this group of species, the alignment of research approaches with the questions considered across species and populations is limited. Additionally, spatial and taxonomic heterogeneity in research effort limits our confidence in assessing the impacts of climate change on this vulnerable group.

4.1. Research biases and knowledge gaps

4.1.1. Regional study effort

This study focussed on temperate seabird species which breed in the UK and Republic of Ireland; therefore, it does not fully represent study efforts for Arctic and Mediterranean species that also inhabit peripheral areas of the North-East Atlantic. Among the seabird species examined, we found disparity in the number of studies between regions within the North-East Atlantic. The North Sea was the most studied region, with the majority of studies arising from the Isle of May. The distribution of seabird breeding populations likely influences the variation in regional study effort. However, for the most frequently studied species in this Review — kittiwake, puffin, guillemot, and shag — breeding populations are widespread across Northern Europe (EBCC 2022, Burnell et al. 2023). This suggests

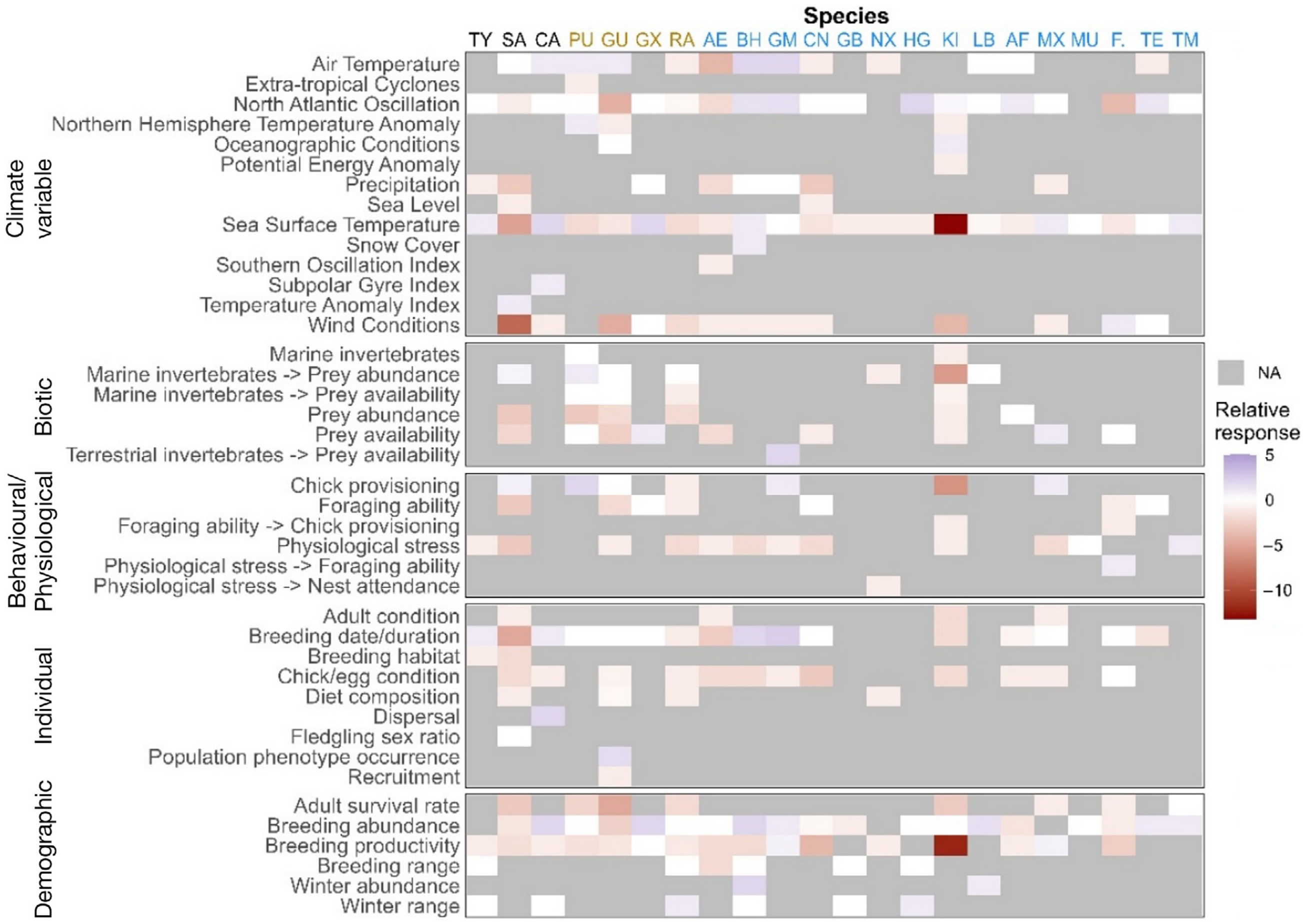

Fig. 4. Relative response index in relation to parameter and species, categorised by parameter groups including climate variables; a biotic covariate; a behavioural or physiological response; an individual-level response; and a demographic-level impact. Cells are shaded from blue (positive) to red (negative) based on the relative response index. Species are coloured by foraging group: benthic foraging (black), midwater foraging (yellow), and surface foraging (blue). Species codes and climate variable definitions are given in Table 1. NA: no studies were available to measure a response

that regional differences in study effort are occurring independently of species distributions.

Given spatial variation in the diets, population trends, and responses to climate that exist between colonies, the response of individual species to mechanistic parameters may not necessarily be applicable to the entire North-East Atlantic. Specifically, colonies within the Celtic Seas are less reliant on sandeels than those in the North Sea and are therefore potentially less vulnerable to a cascade of impacts arising from increasing SST affecting plankton composition (Frederiksen et al. 2005, Cook et al. 2011, Lauria et al. 2012). Spatial variation has been accounted for within some individual studies by comparing colonies that reside within similar (Wanless et al. 2009, Lauria et al. 2013, Lorentsen et al. 2015) and differing seas (Harris et al. 2005, 2006, Frederiksen et al. 2013, Reiertsen et al. 2014). This shows the value of large-scale demographic monitoring schemes (Harris et al. 2024).

4.1.2. Species-level research effort

We found variation in the extent to which different seabird species have been studied in the North-East Atlantic. While guillemot, razorbill, kittiwake, and shag have been reasonably well studied, the majority of surface foraging species (terns, gulls, skuas, and petrels) were the subject of fewer studies, and therefore the degree of confidence in their response to mechanism parameters will be lower. Gaps in published research are prevalent for certain species; this bias is potentially due to the ease of study of a given species. This is highlighted in the contrast in the number of studies between shag (24 studies) and cormorant (5 studies), potentially due to the comparative shyness of cormorants during the breeding season. Species which have been identified as good indicators of marine prey stocks, such as shags (Lorentsen et al. 2015) and kittiwakes (Daunt et al. 2008), have been the focus of more dedicated research. In comparison to guillemots, kittiwakes, and shags, the degree of confidence in the mechanisms identified for understudied species, such as the majority of surface foraging species, will be lower. Therefore, identifying variation or commonality in the responses of seabird species to climate change requires comparative research effort between species. Examples of such a multi-species approach include a comparison of trends in breeding population and success in relation to the NAO index by Reid et al. (1999); a comparison of phenological trends with SST conducted by Burthe et al. (2012); and the effects of multiple climate variables on breeding success investigated by Searle et al. (2022).

4.2. Key mechanisms

4.2.1. Climate indices and prey

In the most studied species (i.e. kittiwake, puffin, guillemot, and shag), SST and NAO were often used to examine climate and were commonly linked to prey abundance or accessibility. NAO was frequently cited as a proxy for at-sea winter conditions, which may affect adult survival, breeding timing, and productivity through pre-breeding adult condition (Wanless et al. 2007, 2009, Frederiksen et al. 2013). A positive NAO is characterised by warm, wet winters and westerly/variable winds. These conditions have been linked to poorer overwinter survival and condition in sandeels (Wanless et al. 2009), a key prey for multiple species within the North-East Atlantic. SST was primarily used to indicate local oceanographic conditions (Álvarez & Pajuelo 2011, Burthe et al. 2012) and phytoplankton habitat suitability (Frederiksen et al. 2013), affecting bottom-up prey abundance. This was most notable in the North Sea, where stochastic shifts in SST cascade through the food chain to reduce the abundance of lipid-rich zooplankton *Calanus finmarchicus*, in turn reducing the abundance and size of sandeel prey (Frederiksen et al. 2013).

4.2.2. Species-specific responses to indirect impacts

Sufficient evidence was available to display a response by kittiwakes, puffin, and guillemot demography to both NAO and SST through bottom-up prey driven mechanisms. However, in shags, another commonly studied species, NAO did not frequently elicit a response, potentially because they are non-migratory and inshore dwelling birds. Kittiwakes, as surface feeders, were often linked to variations in prey abundance (Frederiksen et al. 2006, Wanless et al. 2007), while diving guillemots, which are able to forage throughout the water column, were relatively less affected. Studies frequently attributed negative effects of climate to reductions in prey availability from adverse weather (Votier et al. 2005, 2009, Munilla et al. 2007). For all 3 species (guillemot, shag, and kittiwake), the observed impacts on breeding productivity were all mediated through bottom-up impacts on prey availability or abundance.

4.2.3. Species-specific responses to direct impacts

Weather conditions such as air temperature, wind conditions, and precipitation linked to storms underpin direct, top-down mechanisms by causing breeding failure (Velando et al. 1999, Newell et al. 2015) or adult mortality (Harris & Wanless 1996, Morley et al. 2016). Adverse weather can also impact birds through high winds disturbing incubating adults off eggs, swell washing away nests (Newell et al. 2015), and high rainfall flooding nest burrows (Harris & Wanless 2011); or rising sea levels combined with storm surges flooding low-lying colonies of ground nesting birds (Norris & Buisson 1994, Van De Pol et al. 2010, Palestis & Hines 2015). These conditions may vary in severity in relation to the NAO index, with positive index years linked to increased storminess. Negative impacts from adverse weather conditions were found across foraging groups; the greatest impact from gales is potentially on shag and cormorant, which have only partially waterproof plumage, leaving individuals vulnerable to hypothermia following periods of extreme precipitation (Grémillet et al. 1998). High winds and precipitation may reduce foraging efficiency by impairing foraging and flight ability (Birkhead 1976, Taylor 1983, Finney et al. 1999, Lewis et al. 2015). Through these mechanisms, high precipitation and onshore winds in winter have been found to reduce immature and adult survival (Frederiksen et al. 2008, Bustnes et al. 2013).

4.3. Key vulnerabilities

4.3.1. Bottom-up processes

Through the current available research, the most commonly highlighted mechanisms linking climate change to impacts on seabirds were mediated indirectly through prey populations. Further understanding seasonal and spatial variations in prey throughout a species' range and across its life history may help assess the vulnerability of a population to climate change. The importance of diet is seen in variable kittiwake population trends between the east and west coast of the UK, with more positive trends in the west where sandeels are a smaller component of the diet and responses to changes in SST have been weaker (Frederiksen et al. 2005, Cook et al. 2014). Data on diet from colonies based on the west coast, notably the Irish and Celtic Seas, are needed to be able to explore the relationship of prey availability and seabird demography in areas other than the North Sea, particularly as differing ocean regions will be subject to varying conditions. Critically, this identifies the potential for climate change adaptation interventions that aim to manage the abundance or availability of food resources as a means of counteracting detrimental climate change impacts (Pearce-Higgins & Green 2014). For example, the closure of the North Sea sandeel fishery (Scottish Government 2023) may reduce the loss of key prey for kittiwake populations and offset the negative impacts of warming upon fish abundance (Frederiksen et al. 2004b).

4.3.2. Top-down processes

This study has also highlighted direct impacts of adverse weather conditions on bird mortality and productivity, affecting breeding habitat, or temperature stress contributing to mortality or reduced physiological condition. In the context of negative impacts of storm surges on coastal nesting seabirds, decisions made about coastal management, coastal realignment, and sea defences can also provide opportunities for climate change adaptation to help reduce the vulnerability of key populations to such negative impacts (Bowgen et al. 2022). Due to their *k*-selected breeding strategy, seabirds are generally resilient to occasional breeding failures on a population scale, whereas populations decline much more immediately in response to reductions in adult survival (Ricklefs 1990). However, an increased frequency of extreme weather events directly affecting productivity may cumulatively start to impact breeding abundance if sufficiently chronic over time.

4.4. Recommendations for future research

4.4.1. Survival monitoring

There is an urgent need for further research to understand the impacts of climate change on species and regions which have been relatively poorly studied to date. Species regarded as difficult to study through traditional monitoring techniques may therefore require the application of novel techniques, such as remote sensing camera traps (Black et al. 2018). A focus on certain demographic parameters such as breeding productivity may lead to mechanisms affecting other demographic rates being potentially overlooked, notably survival. Improved knowledge of adult and juvenile survival may be gained through concerted effort to bolster mark—recapture and colour ringing (O'Hanlon et al. 2021), techniques suitable to better understanding long-lived species such as seabirds.

Concerted monitoring of breeding abundance or productivity is required to discern the impacts of climate from events such as disease outbreaks that may have compounding impacts on survival (Blagodatski et al. 2021). However, studying survival in long-lived seabirds with complex age structures is challenging, requiring many years of effort through capture—mark—recapture or resighting studies. The resources required to generate reliable survival data contribute to its scarcity in the current literature, despite the demonstrable importance of survival rates on seabird demography (O'Hanlon et al. 2021). For example, further understanding of adult survival during the winter, and carry-over effects between seasons (Reed et al. 2015), may improve our understanding of climate impacts outside the breeding season when seabirds are generally inaccessible. In the context of climate change, or other environmental changes impacting survival such as avian influenza (Pearce-Higgins et al. 2023), there is an urgent need to support and expand such demographic studies in order to provide more comprehensive assessments of the impacts of climate change on seabird populations.

4.4.2. Short-term vs. long-term studies

The majority of studies selected as relevant to this Review used long-term data sets, as demographic trend data are necessary in understanding the effects of climate change (Oro 2014). However, short-term studies showing the impacts of individual adverse events on colonies, such as storm events (Newell et al. 2015) or heat stress (Oswald et al. 2008, Choy et al. 2021), are valuable, as they display direct mechanisms by which climate affects species. To comprehensively assess the effects of climate on seabird populations, both long-term studies to identify correlative trends between climate variables and demographic patterns, and short-term studies to display the processes driving these impacts, are necessary.

4.5. Conclusions

Despite limitations in comparable study effort between species, regions, and demographic rates, this Review highlights the large extent of published research carried out to date within the North-East Atlantic. While not the focus of many of the studies, the mechanism pathways by which climate influences demography is valuable knowledge to inform adaptation options (further outlined by Pearce-Higgins et al. 2021) to address these mechanisms and counteract negative demographic impacts.

The current body of knowledge has highlighted the importance of climate mediation through the food chain, affecting plankton, fish, and then birds, at least for diving species and kittiwake. Severe storm events may also be a source of physiological stress and inhibit the foraging ability of seabirds. Therefore, our results indicate that climate change adaptation efforts should prioritise 2 key actions: first, improving the management of fish stocks near seabird colonies to preserve food resources, and second, implementing coastal management practices to protect colonies from the impacts of severe storm events.

Pathways of climate impacts on the majority of seabird species remain poorly known and require urgent research. In the context of climate change, we would prioritise the establishment of long-term population monitoring of abundance, productivity, and survival across a range of key sites for different species across their geographical ranges. This would provide long-term data which can then be related to long-term variation in environmental parameters to understand change. Individual, more detailed, studies may then be used to further delve into the underlying mechanism. Such studies may be best achieved through the investment of universities and research institutions at particular sites and populations where more intensive demographic and dietary studies could be undertaken. This could be supported by the efforts of skilled volunteers able to collect data from a wide range of colonies, sites, and species, and contribute to national seabird monitoring programmes, such as the Seabird Monitoring Programme in the UK (Harris et al. 2024) or SEAPOP in Norway.

This Review underscores the urgent need for coordinated research and strategic climate adaptation efforts, emphasizing enhanced monitoring, management of fish stocks, and habitat protection to mitigate climate impacts on North-East Atlantic seabird populations.

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