

SYNTHESIS

Climate change impacts on seabirds and marine mammals: The importance of study duration, thermal tolerance and generation time

Florian Orgeret¹  | Andréa Thiebault¹  | Kit M. Kovacs²  | Christian Lydersen²  |
 Mark A. Hindell³  | Sarah Ann Thompson⁴  | William J. Sydeman⁴  |
 Pierre A. Pistorius^{1,5} 

¹Marine Apex Predator Research Unit (MAPRU), Department of Zoology, Institute for Coastal and Marine Research, Nelson Mandela University, Port Elizabeth, South Africa

²Norwegian Polar Institute, Fram Centre, Tromsø, Norway

³Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, Tasmania, Australia

⁴Farallon Institute, Petaluma, California, USA

⁵DST-NRF Centre of Excellence at the FitzPatrick Institute of African Ornithology, Nelson Mandela University, Port Elizabeth, South Africa

Correspondence

Florian Orgeret and Pierre A. Pistorius, Marine Apex Predator Research Unit, Faculty of Science, Department of Zoology, Institute for Coastal and Marine Research, Nelson Mandela University, South Campus, Port Elizabeth, South Africa.

Email: florianorgeret@gmail.com; pierre.pistorius@mandela.ac.za

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Abstract

Understanding climate change impacts on top predators is fundamental to marine biodiversity conservation, due to their increasingly threatened populations and their importance in marine ecosystems. We conducted a systematic review of the effects of climate change (prolonged, directional change) and climate variability on seabirds and marine mammals. We extracted data from 484 studies (4808 published studies were reviewed), comprising 2215 observations on demography, phenology, distribution, diet, behaviour, body condition and physiology. The likelihood of concluding that climate change had an impact increased with study duration. However, the temporal thresholds for the effects of climate change to be discernibly varied from 10 to 29 years depending on the species, the biological response and the oceanic study region. Species with narrow thermal ranges and relatively long generation times were more often reported to be affected by climate change. This provides an important framework for future assessments, with guidance on response- and region-specific temporal dimensions that need to be considered when reporting effects of climate change. Finally, we found that tropical regions and non-breeding life stages were poorly covered in the literature, a concern that should be addressed to enable a better understanding of the vulnerability of marine predators to climate change.

KEYWORDS

climate change, climate variability, demography, marine biodiversity, marine predators, oceanography, publication biases, sea surface temperature, systematic review, time series

INTRODUCTION

The world's oceans play a central role in climate regulation and in recent decades have absorbed over 93% of the extra heat resulting from the greenhouse effect and about 31% of anthropogenic carbon dioxide from the atmosphere (Bindoff et al., 2019 in the Special Report on the Ocean and Cryosphere in a Changing Climate,

SROCC, IPCC, 2019). This has induced significant and accelerating temperature increases in marine systems globally (Gruber et al., 2019), with potential far-reaching implications for marine biodiversity (Hillebrand et al. 2018; Smale et al., 2019). However, the magnitude and direction of physical changes are highly variable across regions (Hoegh-Guldberg et al., 2014; Hoegh-Guldberg & Poloczanska, 2018) and the underlying natural patterns

of climatic variability are complex, with variable effects on marine biota (e.g. El Niño-Southern Oscillation (ENSO), Stenseth et al., 2002, Stenseth et al., 2003, Brown et al., 2011) complicating the attribution of biological responses at the global scale to long-term climate change.

Owing to their long lifespans and large-scale mobility capabilities, marine top predators, such as seabirds and marine mammals, integrate information from the bottom to the top of the food web and can serve as sentinels of ecosystem change (reviewed by Hazen et al., 2019; Sydeman et al., 2021). By integrating the effects of climate on physical oceanography and the bottom-up impacts on primary and secondary productivity, these taxa provide signals of climate change in their demographic, dietary, distributional and phenological traits (reviewed by Sydeman et al., 2015). Given their consumption of large quantities of prey, these animals also exert significant top-down effects on marine food webs and ecosystem functioning (Hammerschlag et al., 2019). As many seabird and marine mammal species breed on land (or on stable, predictable ice platforms), or need to come to the surface to breathe (e.g. cetaceans), population monitoring is often feasible, and many multi-decadal studies have been implemented in both the northern and southern hemispheres (Hazen et al., 2013; Hindell et al., 2020; Sydeman et al., 2021; Wooller et al., 1992). Furthermore, the effects of climate on these predators appear to be largely indirect, through changes in food webs, oceanic habitats, marine productivity and prey availability (Albouy et al., 2020; Grémillet & Boulinier, 2009; Jenouvrier, 2013; Sydeman et al., 2012, 2015). However, some direct effects are also possible, for example, through changes in their physiology, breeding failure due to adverse conditions at breeding sites or through the influence of extreme events on their foraging ability (Grémillet & Boulinier, 2009; Sydeman et al., 2012, 2015).

Quantitative research syntheses (*sensu* Koricheva et al., 2013) on endothermic marine predators are rare (included in Poloczanska et al., 2013, 2016, and see Keogan et al., 2018, Sydeman et al., 2021). In the case of seabirds, reviews by Sydeman et al. (2012) and Barbraud et al. (2012) showed that seabirds are responding to climate on a global scale through demographic, distributional and phenological shifts, but some responses are inconsistent (Keogan et al., 2018). Some data (from 51 studies) on seabirds and marine mammals were included in the global meta-analyses of marine climate impacts on biodiversity by Poloczanska et al. (2013, 2016), but observational data for marine mammals were especially sparse at the time of their review (only nine studies were included), and in this meta-analysis, data from studies of climate variability were not included.

It is generally assumed that long-term studies are required to be able to observe biodiversity responses to climate change (e.g. Brown et al., 2011; Poloczanska et al., 2013). As a consequence, a number of research syntheses on climate change have restricted their reviews

using a temporal threshold, focusing only on long-term observations. For example, Parmesan and Yohe (2003) and Poloczanska et al. (2013) only included studies with observations that spanned more than 20 or 18 years, respectively, with the specific objective of minimising potential noise resulting from natural climate variability.

Defining a threshold to distinguish between climate change and variability can, however, be problematic when studying disparate ecosystems (Hoegh-Guldberg et al., 2014) or even different populations (Brown et al., 2011) that have been subjected to different rates of climate change. Changes may be most visible and rapid in the Arctic, where significant decreases in sea ice extent have been observed over short time intervals (Meredith et al., 2019). Other ecosystems are also subject to large-scale fluctuations in climate due to, for example, the ENSO cycle in the tropical Pacific (McPhaden et al., 2006; Stenseth et al., 2002). For these regions, longer periods of observation may be required to separate natural fluctuations from long-term climate change (Latif et al., 1997). Nonetheless, even in those ecosystems, studies on climate variability can be informative regarding biological responses to a change in climate. Combined with expected future climate changes (Bindoff et al., 2019), these studies become a valuable contribution to global knowledge on current and expected effects of climate change on marine predators and their ecosystems (Hindell et al., 2020).

Species also can vary greatly in terms of exposure and vulnerability to changing environmental conditions (Albouy et al., 2020; Poloczanska et al., 2013, 2016; Sydeman et al., 2021). Some seabird and marine mammal species are resident year-round in relatively small ranges while others demonstrate remarkable migrations across ocean basins (Hindell et al., 2020). Different life history parameters, possibly related to generation times, as well as niche breadth also influence the ability of species to respond to changing conditions (Sydeman et al., 2015). Understanding the extent to which movement patterns and life history characteristics influence animal responses to climate change is therefore critical to their management and conservation and should be considered in global assessments of climate change impacts on biodiversity (Hillebrand et al. 2018; Hobday et al., 2015; Sydeman et al., 2021).

In this paper, we provide a comprehensive, up-to-date assessment of seabird and marine mammals responses to both climate change and climate variability. In this context, climate variability can be defined as the 'variation in the mean state of the climate beyond that of individual weather events', whereas climate change refers to a 'change in the state of the climate that can be identified by changes in the mean and/or the variability of its properties that persists for an extended period' (definitions from the SROCC, IPCC 2019). We initially map the global distribution of climate studies on seabirds and marine mammals and provide an accompanying online

interactive map. Using resulting data, we empirically identify the study duration required to detect an impact of climate change, in relation to geographic region and biological response. We further investigate the vulnerability of different seabird and marine mammal species to climate change based on their thermal ranges (a proxy for thermal niche) and age at first breeding (a proxy of generation time, a key life history trait). Finally, we present recommendations for future assessments of climate change impacts on endothermic marine vertebrates.

MATERIALS AND METHODS

Systematic review protocol

Using a systematic review (i.e. reproducible) protocol involving available literature as of October 2019, we compared climate effects on seabirds and marine mammals across oceanic regions. Through the ISI Web of Science Core Collection and using relevant keywords (see Supporting Information section 5) including both 'climate change' and 'climate variability,' we developed a database with information extracted from previously published studies. We included all studies with a temporal scale of at least two years. We chose this approach specifically to identify the temporal scale needed to distinguish responses due to climate change and variability.

To summarise, an article had to meet the following criteria for inclusion: (1) include a clear statement that the study objectives were to investigate the potential effects of climate, (2) report on original data analyses (i.e. reviews were not included), (3) include analyses on quantitative relationships between a climate variable and a response variable (usually conducted by correlation), and (4) provide explicit comparisons of changes in response variables in relation to climate through time. In the case of studies with duplicate datasets and updated analyses, we selected only one study with the longest time series, typically the most recent publication. An observation was defined as a biological response variable (demographic parameter, phenology, distribution, behaviour, diet, condition or physiological variable) and a climatic variable [e.g. Sea Surface Temperature (SST) but also including global indices such as Southern Annular Mode or Pacific Decadal Oscillation (PDO), see detailed protocol in Supporting Information sections 4 and 5].

In the absence of standardised measurements for both response and explanatory variables between studies, we did not attempt to synthesise disparate variables and compare the direction of reported effects. However, due to better reporting standards for demography data (which includes population counts, survival estimates and breeding success) and the standardised nature of SST data, we investigated the direction of climate effects (positive, negative, null) according to taxonomic groups and oceanic regions in relation to SST.

Species variation

Thermal tolerances

We constructed thermal distribution ranges for each species included in the review using distribution maps from two of the most comprehensive seabird and marine mammal databases (available from Birdlife, <http://datazone.birdlife.org>, and the International Union for Conservation of Nature, <https://www.iucnredlist.org>). For each species, based on polygons as estimated from distribution maps, we extracted SST values (°C) averaged between 1993 and 2018 (available from Marine Copernicus, global-reanalysis-phy-001-026 product). We calculated SST ranges over the distribution of each species and used these as a proxy for thermal niche. The species were then classified into three groups of thermal ranges ($5 \pm 2^\circ\text{C}$ for narrow, $14 \pm 6^\circ\text{C}$ for intermediate and $24 \pm 6^\circ\text{C}$ for wide ranges) using a kmeans clustering algorithm (see details in Figure S7). We investigated whether species with narrow thermal tolerances showed more responses to climate change (Donelson et al., 2019; Jiguet et al., 2006, 2010).

Life history variation

We also extracted the age at first breeding for every species from two complementary online databases (DATLife available at <https://datlife.org> and the Encyclopedia of Life available at <https://eol.org>) and the Handbook of the Birds of the World (Del Hoyo et al., 1992). We considered this measure as a proxy of generation time (Gaillard et al., 1989, 2005). We then separated species into two groups based on the median age at first breeding (≤ 4 or ≥ 5 years, for both seabirds and mammals, Figure S8). We investigated whether species with a relatively short generation time (and hence to have a higher adaptation rate) were less vulnerable to climate change (Sydeman et al., 2015).

Statistical analyses

All analyses were conducted in R software (R Core Team, version 3.6.1). Results are presented as mean \pm standard deviation.

Vote counting bias-conscious approach

Given the breadth and diversity of the responses and climatic variables measured as well as varied reporting standards in the reviewed studies, we used a 'vote counting' approach to quantitatively summarise the data across disparate studies. This method contains inherent statistical biases (Koricheva et al., 2013) so we used a bias-conscious

approach to limit the impact of those biases on the conclusions reached (Supporting Information section 6). For each observation, we recorded whether the authors reported an effect (1), or not (0), due to climate change, climate variability or both, on the biological responses (i.e. we did not re-evaluate the original interpretations of the authors, see also Poloczanska et al., 2013, 2016).

Effect of study duration: temporal thresholds estimation

In order to empirically estimate the temporal thresholds that would be necessary to separate climate change from climate variability, the dataset was filtered to observations where the climate was reported to have an effect on the response variable (i.e. excluding null effects). Each observation was then coded as (1) classified as climate change or (0) classified as climate variability, according to the authors' interpretations (papers that reported both were excluded).

To allow for non-linear relationships, we used Generalised Additive Models (GAM, 'mgcv' R package, Wood, 2017) with a binomial distribution and a logit link. Responses (change vs. variability) were fitted against a smoother of study duration (as cubic regression splines with shrinkage to avoid over-fitting, Wood, 2017). The starting year of the studies was added as a simple covariate in order to control for potential climate impacts that may have accelerated over time. Based on this model structure, two models were created for each taxonomic group: one model with the response classes as an interaction term to the study duration, and another model with the different oceanic regions as an interaction term with study duration.

Proportion of observations with reported effects

Observations of responses in relation to climate were coded as (1) if an effect or (0) if a null effect was reported by the authors and the resulting data were analysed with Generalised Linear Mixed-effect Models (GLMM, with a binomial distribution and logit link function) using the R package 'lme4' (Bates et al., 2017), in order to compare the observed proportion of (1) and (0) against the null hypothesis that the ratio of the outcomes would be equal (0.5). Each article was assigned a unique ID that was added as a random effect in the models in order to take potential non-independence and pseudo-replication of observations extracted from a single study into account.

RESULTS

We reviewed abstracts from 4808 peer-reviewed research papers that were flagged by our literature search, of

which ~10% ($n = 484$) matched our inclusion criteria. From these papers, 2215 observations were extracted and compiled into a relational CSV database and dynamic map, available online (see data availability section). An average of 4.6 ± 7.4 observations were extracted from each study, involving 2.2 ± 5.1 study species at 1.4 ± 2.3 sites. Substantially more information was available for seabirds ($n = 1685$ observations from 334 articles) compared to marine mammals ($n = 530$ observations from 154 articles).

Although observations on marine mammals were heavily skewed towards the northern hemisphere (83% of observations), there was a similar distribution (54:46%, Northern:Southern) of seabird observations between the two hemispheres (Figure 1). For both groups, there were relatively few observations from tropical and subtropical regions (8% of total), whereas those from the temperate and polar regions represented 53% and 39% of the observations, respectively (Figure 1).

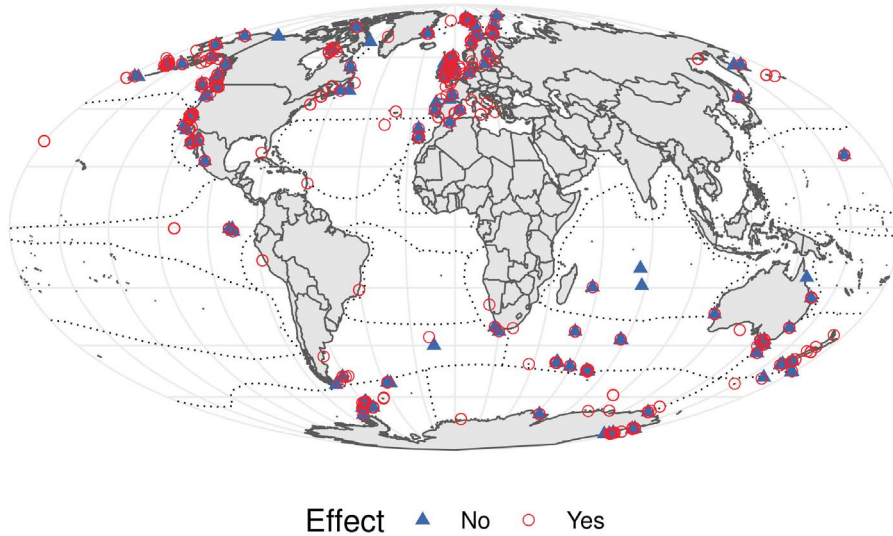
The majority of papers reviewed concluded that climate (either climate change or climate variability) had an effect on both the seabird and marine mammal groups for all the response classes (in total, 68% of observations concluded that there was an effect). For both taxonomic groups combined, 38% of observations were attributed by the original authors to be related to climate change, 49% to climate variability, and 13% to both. More studies concluding that climate change had an effect on marine mammals (57% change vs. 32% variability) as compared to seabirds (32% change vs. 54% variability).

Demographic statistics such as reproductive success and adult survival comprised 54% of the total number of observations. This was the most common response variable studied for both taxonomic groups, but more so for seabirds (60%) compared to marine mammals (34%). Phenology represented the second highest number of observations for seabirds (10%) but was limited for marine mammals (5%). Diet was poorly represented (6% vs. 8%) in both groups. For seabirds, the other classes were relatively evenly represented (7–8% of observations). The physiology class represented less than 0.1% of the compiled observations for both groups ($n = 7$ studies) with only 13 observations and was thus not included further in our analyses.

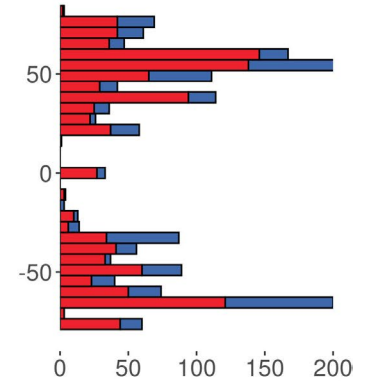
Effect of study duration

Study duration largely explained the probability for original authors to attribute an observed effect to either climate change or climate variability (Figure 2). The longer the study duration, the more likely authors were to conclude that observed changes were due to climate change rather than climate variability, as would be expected. Interestingly, the temporal threshold of 19 ± 5 years for when the effects of climate change were more likely to be discernible (compared to the

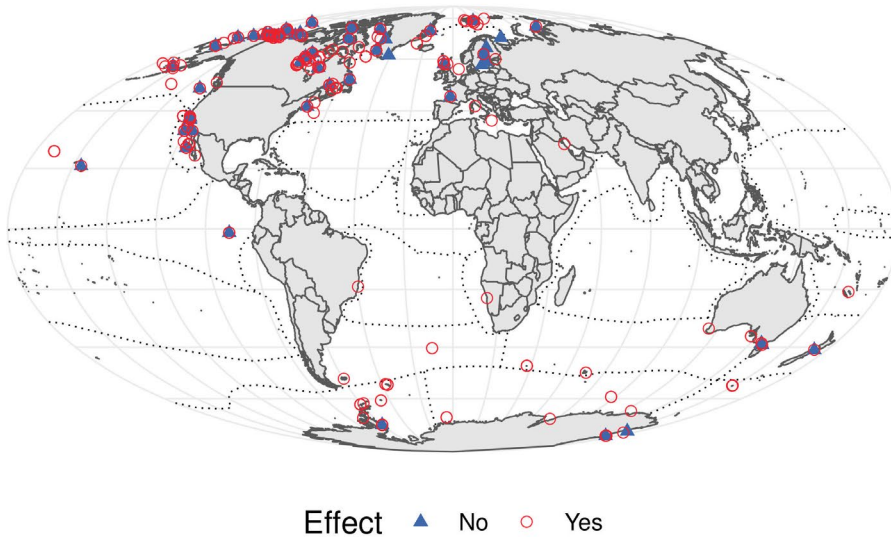
(a) Seabirds



(b)



(c) Marine mammals



(d)

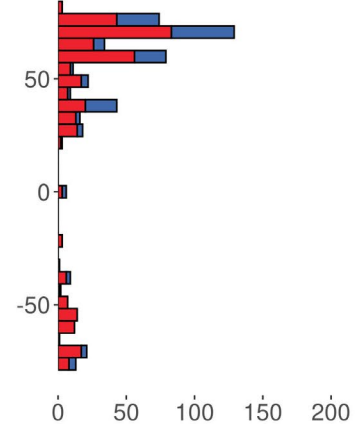


FIGURE 1 Map of the reported effects of climate variability or climate change on (a) seabirds or (c) marine mammals within oceanic regions (dashed lines) as defined in IPCC AR5 (Hoegh-Guldberg et al., 2014). Latitudinal variation in the sample size for (b) seabirds ($n = 1685$ observations from 334 articles) and (d) marine mammals ($n = 530$ observations from 154 articles) is indicated. These data form the basis for the systematic review in this paper and demonstrate unequal sampling between seabirds and marine mammals and geographic regions and hemispheres {See dynamic html map provided as a supplementary file}.

0.5 probability chance) differed by the response variable and the oceanic region under study (Figure 2). In general, studies on marine mammals concluded effects of climate change based on shorter time series (17 ± 5 years) compared to seabirds (22 ± 3 years, Figure 2). The shortest temporal threshold (10 years) that would be needed to detect climate change was observed for Arctic marine mammals, and the longest (29 years) was for tropical seabirds (Figure 2a).

When only considering climate change studies (47% of total), a larger proportion of observations reported

significant effects for the studies with a time span above the estimated average threshold of 19 years (Figure 3a). This was evident for all the biological responses, except for the phenology class where the pattern seemed to be reversed (Figure 3a). Overall, 189 studies (with 669 observations) that concluded on an effect were above this threshold (Figure 3a), which represents 39% of the total number of studies (and 30% of the observations). When studied per taxonomic group, no significant difference could be found in the proportion of studies that reported an effect of climate change between seabirds and marine

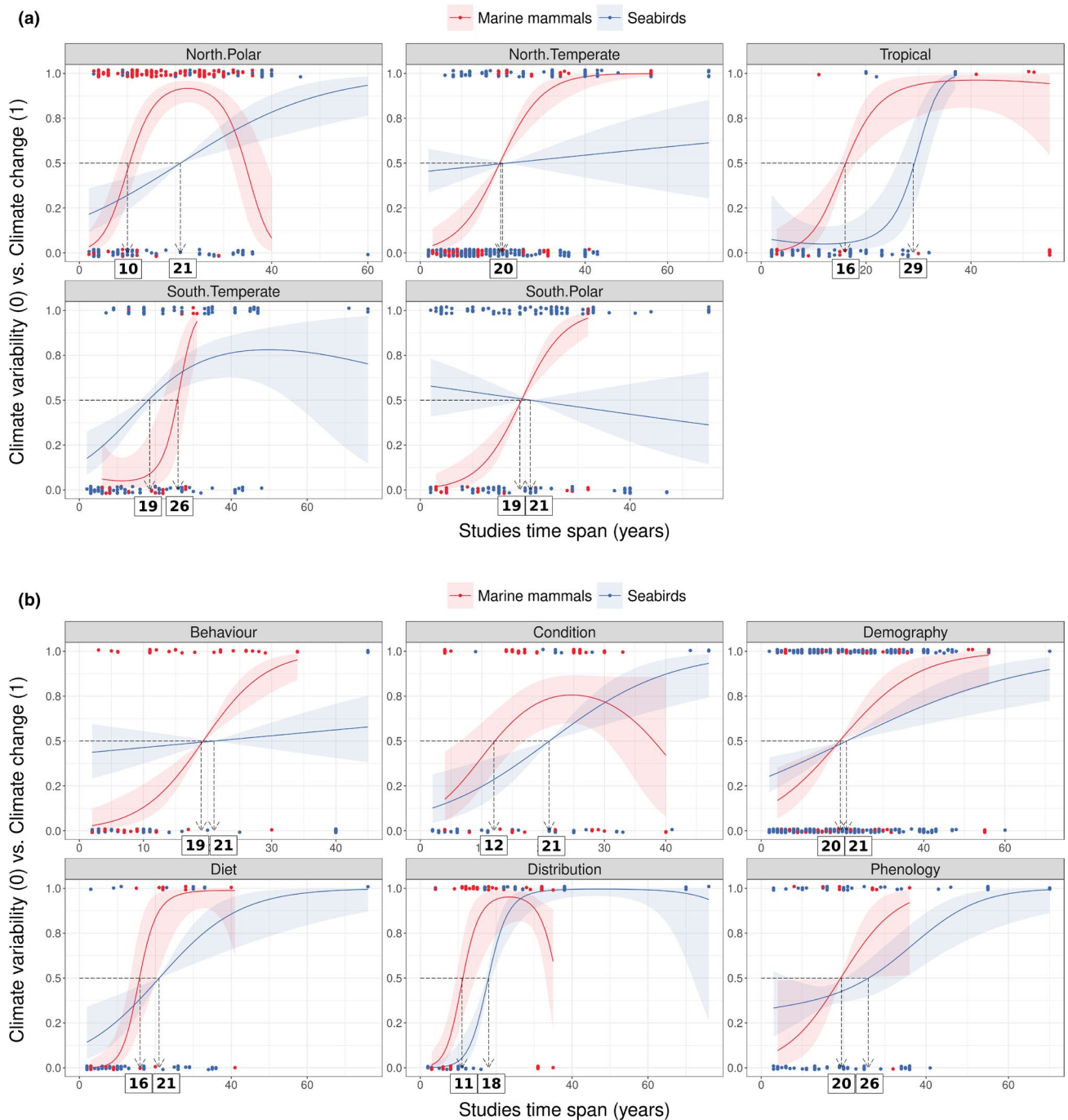


FIGURE 2 Modelled effects of study duration and authors' attributions of climate variability (0) or climate change (1) with two separate models: per oceanic region (a) or per response variable (b) each with seabirds (blue) and marine mammals (red). Studies concluding on both climate change and climate variability ($n = 294$) simultaneously and those concluding no effect ($n = 1269$ observations) were excluded from this analysis. Studies with a time span longer than 100 years (influential points) were removed (12 observations). The mean probabilities (blue and red lines) and 95% confidence intervals (shaded area) of attribution to climate change vs. climate variability were estimated using Generalised Additive Models (Deviance Explained respectively of 10.7% and 16.3% for seabirds and mammals in (a) and 11.9% and 26% for seabirds and mammals in (b)). The equal probability of 0.5 (dashed lines) is used to estimate the minimum time span thresholds that would be necessary to be able to separate Climate Variability from Climate Change (dashed arrows). Estimated thresholds are indicated by boxes on the x-axis. Regions (a) or response variables (b) with non-significant (p -values < 0.05) smoothers resulted in linear relationships

mammals, and the majority of these proportions for all biological responses were significantly higher than 0.5 (Figure 3b). Only the classes phenology for marine mammals and behaviour for seabirds were not significantly

different (Figure 3b). Overall, a significant majority of observations concluded that climate change had an effect on both the seabird and marine mammal groups for all the response classes (Figure 3).

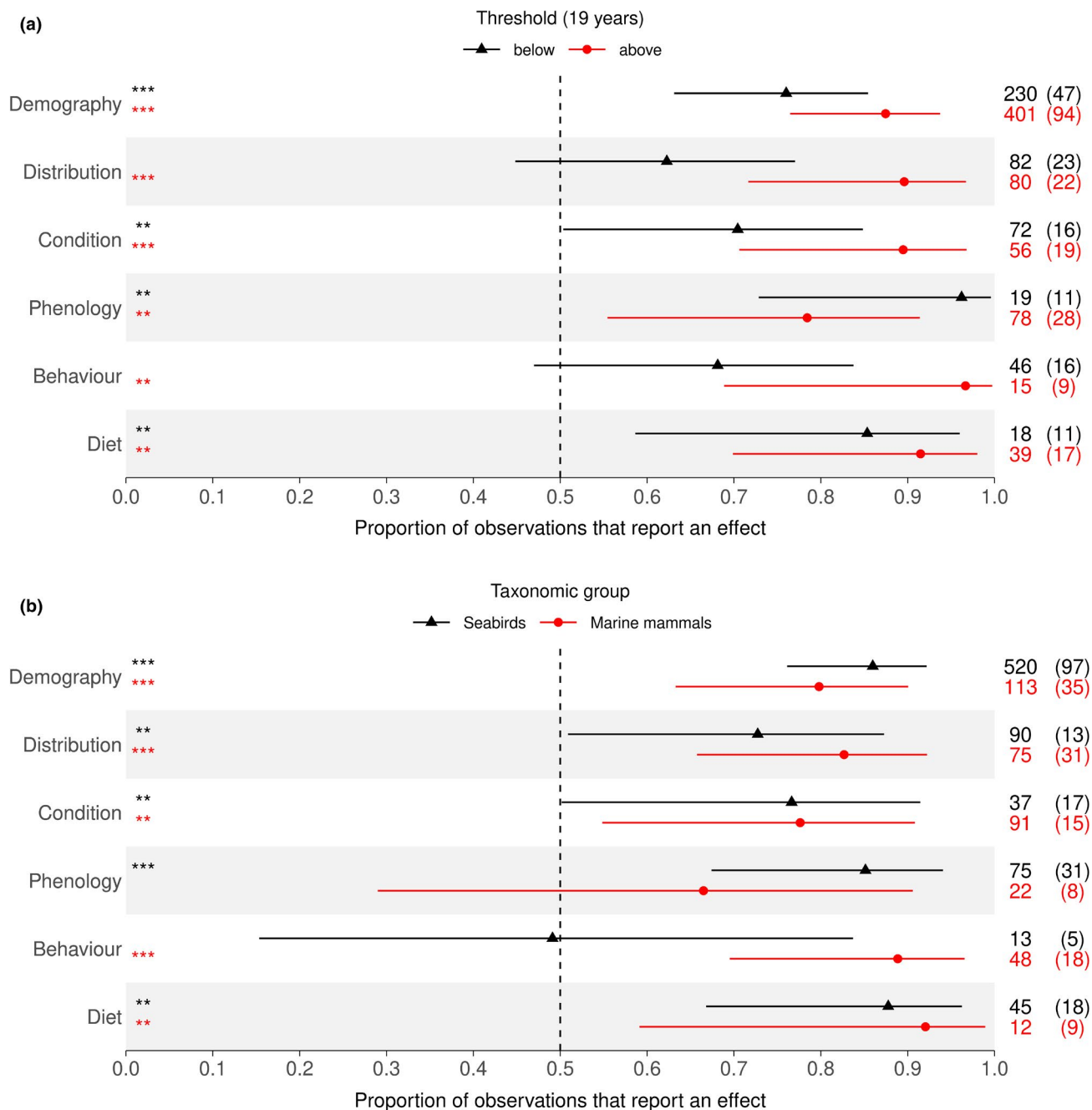


FIGURE 3 Modelled effects of climate change (including only observations relating to Climate Change, i.e. excluding Climate Variability); the dashed line reflects what is expected by chance (0.5). A number of observations (and in brackets the number of studies) are given on the right-hand side of the figure. The proportion of observations having reported a climate change effect in (a) were estimated using two different GLMMs according to observations that were above or below the average duration threshold (estimated from the thresholds in Figure 2) with both seabirds and marine mammals pooled together. In (b) two different GLMMs were used: one for seabird and one for marine mammal observations

Species variation

In terms of species representation, observations involved 235 species (176 seabirds and 59 marine mammals, Figure 4). This covers 41% of the total number of species that belong to the taxa on which the search was conducted (Table 1, see data availability section). Polar bears, *Ursus maritimus* ($n = 185$), Adélie penguins,

Pygoscelis adeliae ($n = 116$) and black legged kittiwakes, *Rissa tridactyla* ($n = 100$) had the highest number of observations (Supporting Information section 9.2, Figure S2). The vast majority of studies were conducted on adults during the breeding season (herein, we consider chick-related variables to be consequences of parental care). Only 14% of observations were from the non-breeding period, and revealingly, less than 0.04% were

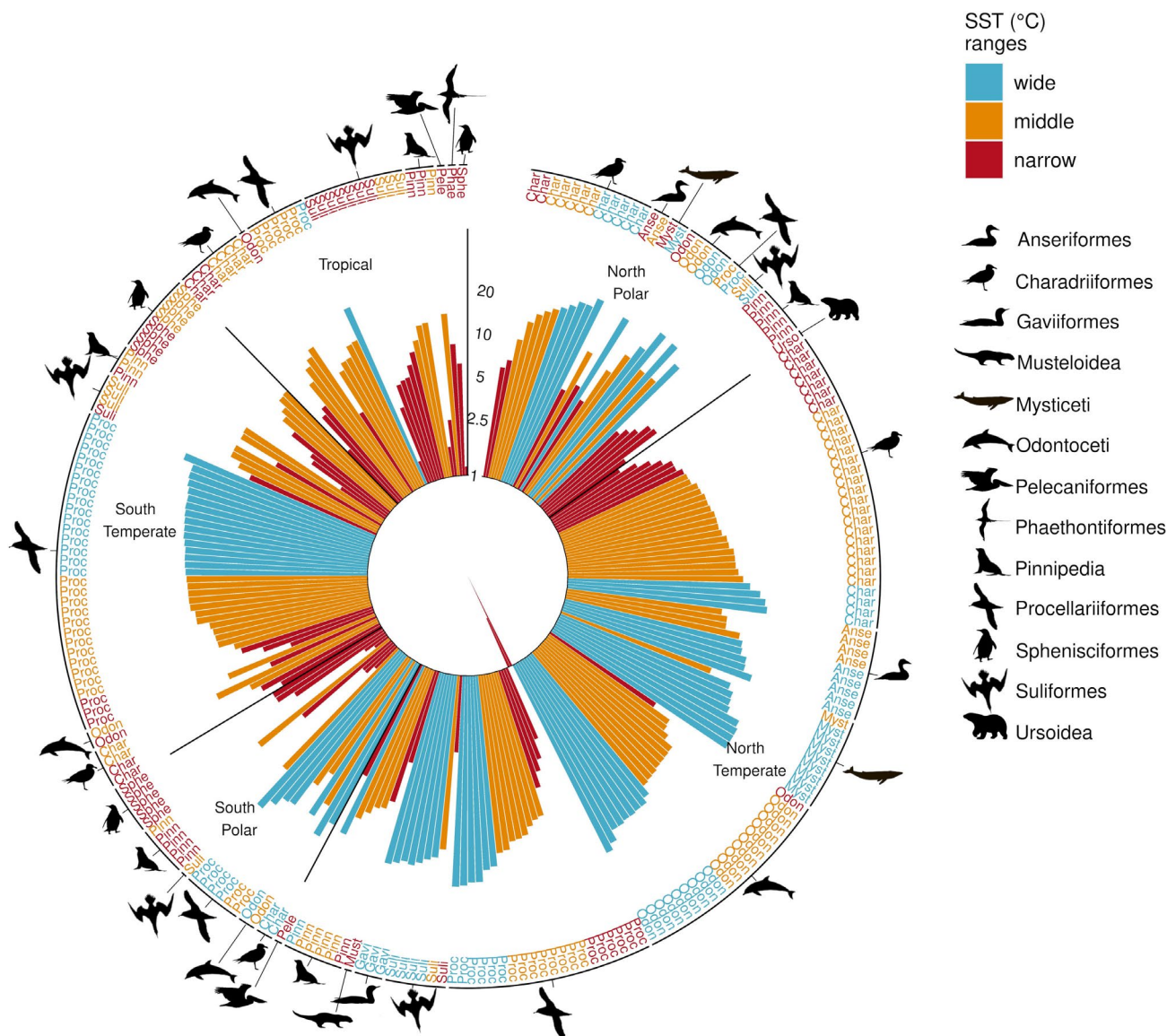


FIGURE 4 Classification of species according Sea Surface Temperatures (SST) within their distributional ranges and oceanic regions (species with narrow SST ranges are expected to more sensitive to climate change). Each bar represents one species (arranged by the order name and illustrated by pictograms). SST ranges have been log-transformed to help visualisation

in early life stages (juveniles, i.e. first year of independence or immatures, before their first breeding attempt); the limited available data on young animals were mostly based on albatrosses, petrels, penguins and seals.

Thermal range

Thermal tolerances varied greatly between species and were dependent on oceanic regions (Figure 4). When grouped into three thermal (SST) ranges, it was clear that most of the narrow range species were situated in the North Temperate (31%) and Tropical (25%) regions. Species with wide thermal ranges were mostly situated in North Temperate (50%) but also in South Temperate (26%) regions. In terms of proportions within each region, narrow

range species were the most represented group in the Tropical (44%), South Polar (36%) and North Polar (41%) regions, and they were less represented in the Temperate regions (22% in the South and 19% in the North).

For all three thermal groups, the proportion of observations that reported on a climate change effect was significant for the demography class (Figure 5a). For all the other classes, the proportions for either the species with a wider or a middle thermal range, or both, were not significant. More specifically, for the behaviour, condition and diet response classes, both middle and wide range species seemed to have been less impacted by climate change as the proportion of reported effects were not different from 0.5 (but see marginal significance for diet for wide range species, Figure 5a). In comparison, a significantly greater proportion of studies on species with narrow thermal

TABLE 1 Proportion of the number of species involved within the reviewed studies compared to the number of species existing for each family

Taxonomic group	Order	Family	Reviewed species	Narrow thermal species	Existing species	Species coverage (%)	
Marine mammals	Odontoceti	Ziphiidae	1	0	24	12	
	Odontoceti	Phocoenidae	2	0	8	25	
	Odontoceti	Kogiidae	1	0	3	33	
	Odontoceti	Delphinidae	17	3	41	41	
	Odontoceti	Monodontidae	1	1	2	50	
	Pinnipediformes	Phocidae	12	8	23	52	
	Pinnipediformes	Otariidae	9	4	17	53	
	Mysticeti	Balaenopteridae	6	0	10	60	
	Mysticeti	Balaenidae	4	1	4	100	
	Mysticeti	Eschrichtiidae	1	0	1	100	
	Pinnipediformes	Odobenidae	1	1	1	100	
	Odontoceti	Physeteridae	1	0	1	100	
	Seabirds	Procellariiformes	Hydrobatidae	10	4	41	24
		Pelecaniformes	Pelecanidae	2	2	8	25
		Suliformes	Phalacrocoracidae	13	4	52	25
Charadriiformes		Laridae	36	8	114	32	
Phaethontiformes		Phaethontidae	1	1	3	33	
Procellariiformes		Procellariidae	40	3	114	35	
Suliformes		Fregatidae	2	2	5	40	
Procellariiformes		Diomedidae	15	3	27	56	
Gaviiformes		Gaviidae	3	0	5	60	
Shenisciformes		Spheniscidae	14	10	23	61	
Charadriiformes		Stercorariidae	6	0	8	75	
Charadriiformes		Alcidae	19	7	25	76	
Suliformes		Sulidae	8	3	10	80	

Species lists were retrieved from the Integrated Taxonomic Information System and National Centre for Biotechnology Information databases with a total of 570 species. The families Ursidae, Mustelidae, Anatidae were excluded because most species in these families are not marine.

ranges reported climate change impacts in all response classes, except for phenology (Figure 5a).

Generation time

Observations for longer-lived species (characterised by an older age at first breeding) were more often reported with an effect of climate change for all response classes on average, except for the phenology response class (Figure 5b). For behaviour and condition, shorter-lived species seemed to have been less impacted by climate change as the proportion of reported effects was not different from the 0.5 chance (but the sample size was low for the behaviour class, Figure 5b).

Direction of demographic effects in relation to SST

Most of the observations involved demographic responses in relation to SST (16%, see Supporting

Information section 9.3. and Figure S3 for a global overview of climatic variables). However, when there was an effect, a greater proportion concluded that the animals were impacted negatively (38%) or not impacted (38%) across the different regions (Table 2, Figure 6). However, in some cases, an increase in SST had a positive effect (24%) on the demography of marine predators, particularly within the Suliformes, Sphenisciformes, Mysticeti and Procellariiformes (Figure 6). For Charadriiformes, sufficient information was only available in the northern hemisphere and a negative effect of an increase in SST was mostly reported, independent of the oceanic region where the study was conducted (Arctic, North Atlantic, Northwest and Northeast Pacific). Suliformes in the northern hemisphere showed more variable responses, with a majority of studies reporting a negative effect in the Northeast Pacific while more studies reported a positive effect in the North Atlantic. Procellariiformes also showed variable responses: mostly positive in the North Pacific and mostly negative in the tropical Pacific, West and East Antarctic and in the sub-Antarctic. Responses

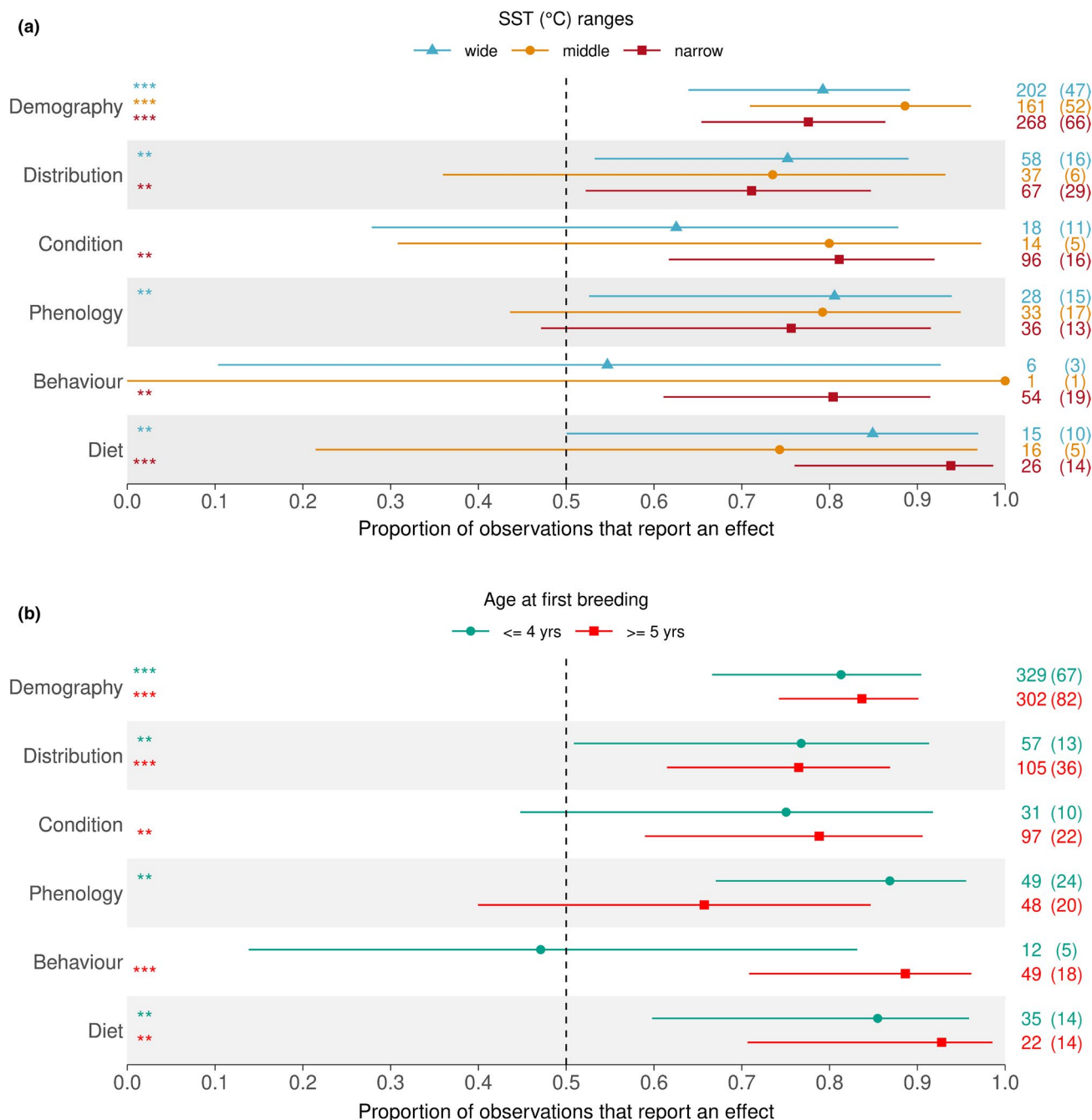


FIGURE 5 Modelled effects of climate change (on seabirds and marine mammals); the dashed line reflects what is expected by chance (0.5). Number of observations (and in brackets the number of studies) are given on the right-hand side of the figure. The proportion of observations having reported a climate change effect were estimated using three GLMMs for each SST distributional range (wide, middle and narrow) of the species (a) and two GLMMs for each age of first breeding classes: shorter-lived vs. longer lived (b). Significance is indicated by stars * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

for this group were inconclusive (high proportion of null responses or similar proportions of positive vs. negative responses) in the Indian and Pacific sectors of the sub-Antarctic and the North Atlantic. Sphenisciformes were more negatively impacted in East Antarctica and in the Indian and Pacific sub-Antarctic regions as compared to West Antarctica and the Atlantic sub-Antarctic region. Relatively few climate-related studies on marine mammals incorporated SST (Table 2, Figure S3).

DISCUSSION

Our study produced a comprehensive database that we used to assess both seabird and marine mammal responses to changing climatic and corresponding oceanographic conditions. Marine mammals were poorly represented in the climate change literature compared to seabirds, with most studies focused on the Arctic (Figure 1). Increasing study duration was positively

TABLE 2 Examples of observations spanning over 19 years for Marine mammal (MM) and Seabird (SB) populations for Demography responses (as in Figure 6, restricted to Breeding success, Population size and Survival) in relation to Sea Surface Temperature (SST), within different geographical regions. Shaded rows help to visualize changes of regions.

Region	Group	Time span	Species names	Thermal range	Effect direction	Brief summary	References
NP	SB	36	Black legged kittiwake	W	Neg	Steep population decline was associated to abrupt warming in SST rates	Descamps et al. (2017)
NP	SB	26	Thick billed murre	W	Null	Adult survival was not correlated to SST	Fluhr et al. (2017)
NP	SB	21	Thick billed murre	W	Neg & Pos	Adult survival was negatively correlated to SST but positively with breeding success	Smith and Gaston (2012)
NT	SB	32	25 species	W & M	Neg & Null & Pos	Population sizes, adult survival or breeding success negatively correlated to increase in SST for half of the species	Burthe et al. (2014)
NT	SB	32	4 species	W & M	Neg & Null	Breeding success negatively correlated to SST for 2 sites but not for 2 species in one site	Byrd et al. (2008)
NT	SB	29	Black legged kittiwake	W	Pos	Breeding success positively correlated to SST (when prey as model covariate)	Carroll et al. (2017)
NT	SB	19	Black legged kittiwake	W	Neg & Null	Breeding success negatively correlated to SST in 2 out of 8 sites	Carroll et al. (2015)
NT	SB	19	Black legged kittiwake	W	Neg & Null	Breeding success globally negatively correlated with SST but regionally only in 2 of 6 sites	Frederiksen et al. (2007)
NT	SB	24	Great cormorant	W	Neg	Breeding success negatively correlated to SST	Gienapp et al. (2012)
NT	SB	19	Atlantic puffin	W	Neg & Pos & Null	Adult survival negatively correlated to SST in 3 out of 4 sites and positively for another site	Harris et al. (2005)
NT	SB	22	4 species	W & M	Neg & Null	Breeding success correlated negatively with SST for 1 of 4 species	Lauria et al. (2012)
NT	SB	32	Lesser black backed gull	W	Pos	Population size correlated positively with SST through food web change	Luczak et al. (2012)
NT	SB	61	Common guillemot	M	Null	Population crash was correlated to SST but to human-related factors	Munilla et al. (2007)
NT	SB	27	Common guillemot	M	Null	Change in population size not correlated to SST but more to human-related factors	Regular et al. (2010)
NT	MM	[19;36]	Grey whale	W	Null & Pos	Calf counts positively correlated to SST in 2 out of 3 sites	Shelden et al. (2004)
NT	SB	31	Scripps's murrelet	N	Neg	Breeding success negatively correlated to SST (associated with lower draught index)	Thomsen et al. (2019)
NT	SB	26	3 species	W & M	Null	Breeding success not correlated to SST (but negatively correlated to late arrival of 13°C isotherm within foraging range)	Watanuki et al. (2012)
NT	SB	26	Cassin's auklet	M	Neg & Null	Breeding success and adult survival negatively correlated to SST	Wolf et al. (2010)

(Continues)

TABLE 2 (Continued)

Region	Group	Time span	Species names	Thermal range	Effect direction	Brief summary	References
T	SB	48	3 species	2 M & 1 N	Neg & Null	Population size negatively correlated for 2 out of 3 species	Barbraud et al. (2018)
T	MM	[41;52]	Northern elephant seal	M	Neg & Null	Pup number negatively correlated to SST	García-Aguilar et al. (2018)
T	SB	20	Audubon's shearwater	M	Pos	Adult survival positively correlated to SST	Precheur et al. (2016)
T	SB	22	Galapagos penguin	N	Neg	Population size negatively correlated to SST	Vargas et al. (2006)
ST	SB	25	Amsterdam albatross	N	Null & Quadratic	Breeding success not correlated to SST but adult survival quadratic relationship with SST	Barbraud et al. (2011)
ST	MM	85	Southern sea lion	M	Neg	Pup number negatively correlated to SST	Baylis et al. (2015)
ST	SB	31	Little penguin	N	Pos	Breeding success positively correlated to SST	Cullen et al. (2009)
ST	SB	33	Yellow eyed penguin	N	Neg	Adult and fledging survival negatively correlated to SST	Mattern et al. (2017)
ST	SB	71	Southern rockhopper penguin	M	Neg	Population size negatively correlated to SST	Morrison et al. (2015)
ST	SB	41	Wandering albatross	W	Neg	Adult survival negatively correlated to SST	Pardo et al. (2017)
ST	SB	22	7 species	1 W, 3 M, 3 N	Null	Population size not correlated with SST	Raya Rey et al. (2014)
ST	SB	25	Amsterdam albatross	N	Null	Adult and juvenile survival not correlated with SST	Rivalan et al. (2010)
ST	SB	25	Black browed albatross	W	Pos	Adult survival positively correlated with SST	Rolland et al. (2008)
SP	SB	20	Emperor penguin	N	Neg & Null	Adult survival negatively correlated to SST but not breeding success	Barbraud and Weimerskirch (2001)
SP	SB	27	3 penguin species	N	Null & Pos	Population size positively correlated with SST for 1 of 3 species	Lima et al. (2013)

Regions: North Pole (NP), South Pole (SP), North Temperate (NT), South Temperate (ST), Tropics and subtropics (T). Effect direction: Positive (Pos), Negative (Neg), Null. Thermal range: Wide (W), Middle (M), Narrow (N). Reference list is provided in Supporting Information.

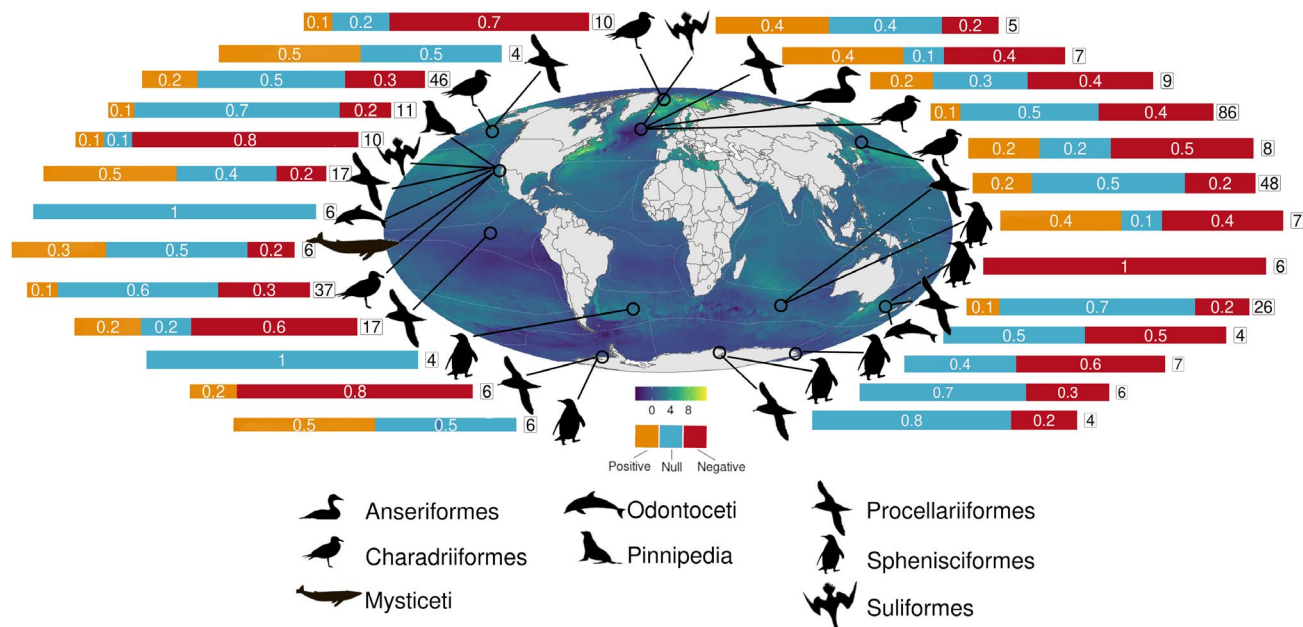


FIGURE 6 Proportions of the direction of the effects for demography responses (survival, population sizes and breeding success) in relation to Sea Surface Temperature (SST) for taxonomic orders that have at least four observations. Number of observations are indicated on the right side of each bar. Ocean colour background indicates, for each pixel, the slope ($\times 10^{-3}$) of linear regression of the sea surface temperature time series 1993–2018 (Marine Copernicus, global-reanalysis-phy-001-026 product)

related to the likelihood of authors to conclude that observed responses were due to climate change rather than climate variability. Interestingly, the temporal threshold of study duration was dependent on both the response variable as well as the oceanic study region (Figure 2). Except for seabird behaviour and marine mammal phenology, a significant majority of studies identified climate change effects on all of the response variables studied (Figure 3b). When looking at the direction of demographic effects, most studies reported either a negative or no response to an increase in SST (Figure 6), but this varied according to the geographical region. Moreover, we demonstrated that species with narrow thermal ranges, and those that had relatively long generation times, were more vulnerable to the effects of climate change (Figure 5).

The importance of study duration

Long-term data series are necessary to separate influences of natural fluctuations from anthropogenic forcing (Brown et al., 2011; Sydeman et al., 2015). The restricted duration of most available datasets poses a significant limitation to studying climate change and biodiversity, especially for long-lived animals such as seabirds and marine mammals (Poloczanska et al., 2013, 2016). Advances in statistical techniques (reviewed in Brown et al., 2011) may enable the separation of variability from trends in time series data in ecology, climatology and oceanography (Stenseth et al., 2003) and may lead to an increase in studies

attributing effects to climate change (see Figure S6). Because marine predator populations are known to display periodicity in breeding performance in association with environmental cycles (reviewed by Stenseth et al., 2002, e.g. Crocker et al., 2006), investigation of oscillating signals (i.e. global indices) and short-term climate variability provides substantial opportunities to predict marine predator responses to climate change (Barbraud et al., 2012; Sydeman et al., 2012, 2015; Trathan et al., 2007). Scenarios based on climate models and associated oceanographic changes describe possible changes in future environmental variables (e.g. Jenouvrier et al., 2021). Notably, models of ocean change also predict an increase in the variability of many environmental conditions, which could potentially affect populations more than an increase in mean conditions (e.g. Piatt et al., 2020). This could be due to an increased frequency of extreme events (Nijse et al., 2019; Thorton et al., 2014; Vasseur et al., 2014) or an underlying increase in baseline values which simply make high values in conditions (e.g. temperature) appear more extreme (Bindoff et al., 2019; Oliver et al., 2018). For this, long-term data are necessary, not only to capture trends but also to be able to separate the impacts of variability (variance) and cyclicality in climatic conditions (such as associated with PDO, North Atlantic Oscillation, or ENSO, see Stenseth et al., 2003) from those induced by directional forcing (Vasseur et al., 2014). In this context, future studies on marine predators will benefit by focusing on the impacts of changes in the variance of environmental variables, and not only their averages. Our approach did not allow us to

separate these mechanisms and these effects need further investigation.

Nonetheless, our results raise important considerations regarding the duration of studies needed to robustly detect climate change effects. The average time that we estimated to be necessary for this distinction was 19 ± 5 years, based on both taxonomic groups, for all response classes and oceanic regions. Interestingly, this average temporal threshold corresponds to the minimum time period that was used by Poloczanska et al. (2013, 2016) to include in their meta-analysis. Importantly, we demonstrated that the time required to detect climate change effects varied considerably depending on the type of response and the oceanic region. Globally, the shortest duration to detect climate change, ~ 10 years, was observed within the Arctic for marine mammals, a reflection of the rapid environmental changes in this region (Gilg et al., 2012; Laidre et al., 2015; Meier et al., 2014; Post et al., 2013; Tynan & Demaster, 1997).

Another factor that could cause difficulties in detecting climate change effects is low sample size (Brown et al., 2011; O'Connors et al., 2015). Indeed, we have shown that when controlled by differences in sample size, the proportions of detected effects decrease significantly (Supplementary Information sections 6.2 and 9.5, Figure S5). This confirms that statistical power is required to detect climate change effects (O'Connors et al., 2015), underscoring the importance of properly reporting sampling effort in studies of climate impact on marine predators. These results will hopefully serve as a guide for future studies on climate impacts on marine predators (Figure 7, Box 1).

Ocean warming: regional and taxonomic demographic differences

Demography was the response class for which studies of the longest duration were available (Figure 2b), with 94 studies extending beyond the 19-year threshold (Figure 3a). Demographic responses were most often assessed in relation to changing SST with most studies reporting a negative relationship, especially in regions that had ocean warming over the last few decades (Bindoff et al., 2019, Figure 6). Most of these studies suggested that ocean warming mainly influenced reproductive success and/or survival through indirect effects via bottom-up processes impacting prey quality or availability (Barbraud et al., 2012; Beaugrand, 2015; Sydeman et al., 2021). However, important differences in the direction of this effect were evident between taxonomic groups, populations and oceanic regions (Table 2, Figure 6). For example, in the North Sea, the majority of a wide range of seabird species (26 species) for which long-term monitoring data (36 years) were available demonstrated a negative response in population size, breeding success or adult survival with increasing SST (Burthe et al.,

2014). Despite the fact that SST has increased markedly in this region, however, 11 species also had positive or no relationships with SST (Burthe et al., 2014). In Alaska, a long-term study (40 years) demonstrated that population growth rates of five seabird species at four different monitoring sites were also most often, but not consistently, negatively associated with SST (Goyert et al., 2018). In southern Argentina, no relationship was detected between population sizes and SST for seven seabird species over 20 years (Raya Rey et al., 2014). In Antarctica, adult survival, population size and/or reproductive success of four penguin species showed varied responses to increases in SST (Barbraud & Weimerskirch, 2001; Lima & Estay, 2013). In Antarctica, adult survival, population size and/or reproductive success of four penguin species showed varied responses to increases in SST (Barbraud & Weimerskirch, 2001; Lima et al., 2013). Even within an ecosystem, varied effects of SST can be observed. For example, breeding success was negatively correlated to SST for populations of Cassin's auklet, *Ptychoramphus aleuticus* in the southern California current, but positively affected in the northern California current (Wolf et al., 2010).

Very few long-term relationships between demographic parameters and SST were found for marine mammals (Table 2). Available studies reported negative, no or positive relationships between the number of pups or calves and increased SST for grey whales, *Eschrichtius robustus*, northern elephant seals, *Mirounga angustirostris*, and southern sea lions, *Otaria flavescens* (Baylis et al. 2015; García-Aguilar et al. 2018; Shelden et al. 2004). Rather, marine mammal demography has mainly been reported in relation to sea ice changes (reviewed in Supporting Information section 10). For example, a reduction in Arctic ice cover has been directly associated with declining body condition and pup production in ringed seals, *Pusa hispida* (Laidre et al., 2015). Changes in sea ice patterns are also driving demographic changes in polar bears, including a decline in some populations where sea ice reductions are most notable (Lunn et al., 2016; McCall et al., 2015). In contrast, increased productivity levels related to reduced sea ice and increased temperatures seem to be creating conditions that are increasing populations of bowhead whales, *Balaena mysticetus* (George et al., 2004; Heide-Jørgensen et al., 2007). Southern elephant seals, *Mirounga leonina*, have also responded demographically (wean mass, first year survival and fecundity) in response to environmental variation related to changes in sea ice extent (Clausius et al., 2017) and the position and depth of the Circumpolar Deep Water (Hindell et al., 2017), both of which are responding to warming conditions.

Interestingly, in several cases (4% of the observations), the relationship between demographic responses and SST was found to be non-linear (e.g. Barbraud et al., 2011; Barbraud et al., 2018; Denhard et al., 2013; Jenouvrier et al., 2018), suggesting that

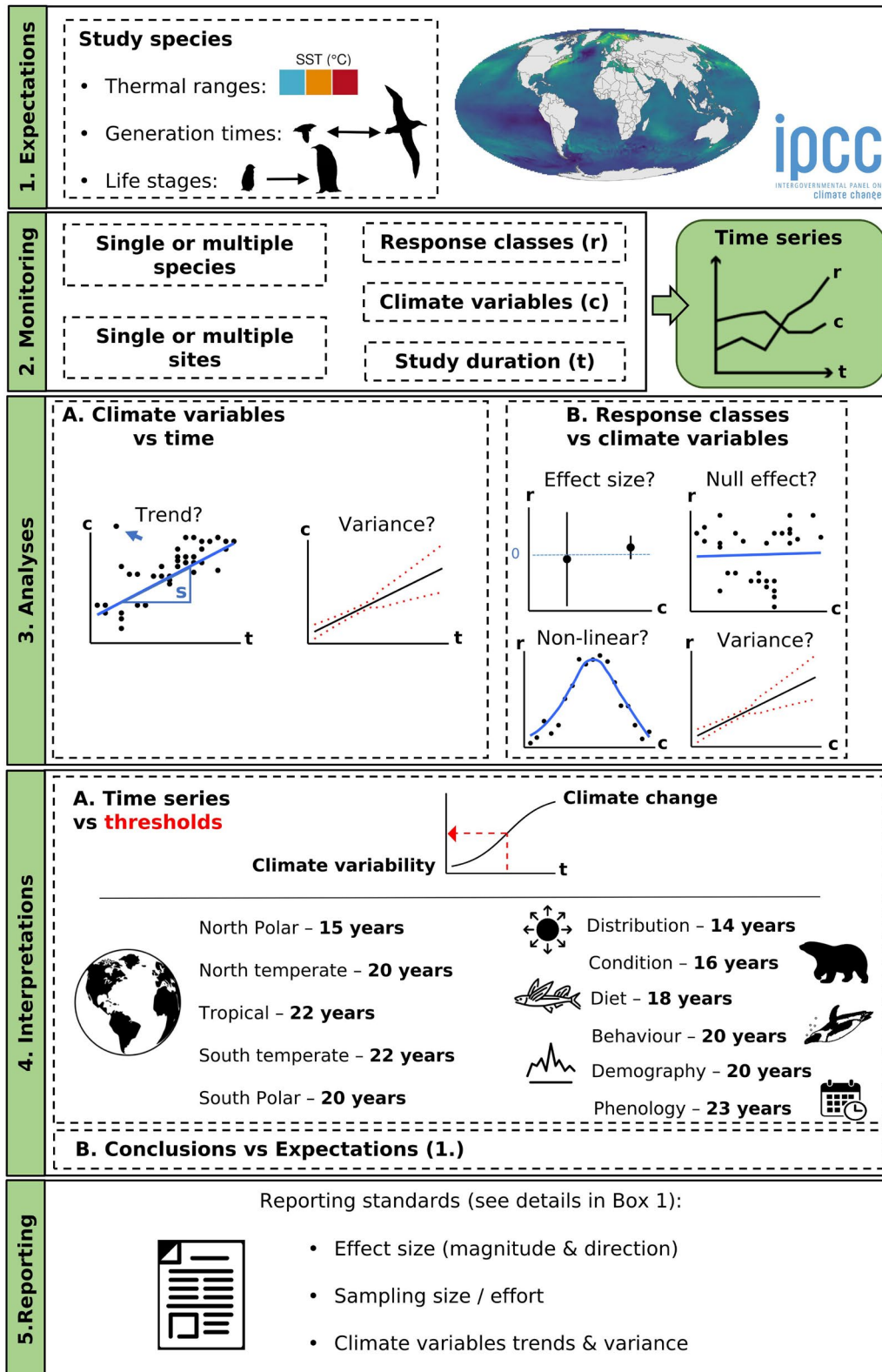


FIGURE 7 Recommended steps (1-4) for conducting a study on the effects of climate change and/or variability on marine predators and a guideline on results to be reported (5). Expectations are particularly important in attributing effects of climate change and can be based on prior knowledge on study species (from existing studies, experiments or historical changes, see details in O'Connor et al., 2015) in relation to regional climate change reported by the Intergovernmental Panel on Climate Change (IPCC). Well-reported studies (and/or with open access data) can then be combined in meta-analyses to quantify and synthesise global processes to confirm/reject hypotheses and expectations

Box 1 Recommendations & knowledge gaps

Reporting standards (to be clearly state in the abstract):

- Study species
- Study location
- Dates of study and time span
- Sampling effort (sample size, number of individuals studied)
- Breeding stage (at least breeding or non-breeding)
- Age classes (at least juvenile or adult)
- Effect size (direction and magnitude)
- Climate variable trends and variance

To limit publication biases

- Multi-species (as opposed to single-species)
- Multi-sites (as opposed to single-site)

Poorly covered:

- **Families** (order name in brackets, see Figure 4)

- Ziphiidae (Ondotoceti)
- Phocoenidae (Ondotoceti)
- Kogiidae (Ondotoceti)
- Monodontidae (Ondotoceti)
- Eschrichtiidae (Mysticeti)
- Odobenidae (Pinnipedia)
- Pelecanidae (Pelecaniformes)
- Phaethontidae (Phaethontiformes)
- Fregatidae (Suliformes)

- **Life stages**

Non-breeding period

- **Age classes**

Pre-breeding life history stages

- **Biological response variables**

Physiology, diet

- **Geographical regions**

Tropical and subtropical

- **Climatic variables**

- Precipitation (snow and rainfall)
- Extreme events (e.g. storms, hurricanes, heat waves)
- Wind
- Ocean chemical properties (e.g. acidification, salinity, oxygen concentration)
- Air temperature

the response only varies across a small range of environmental conditions (Barbraud et al., 2012). Such non-linear relationships could explain the contrasting effects observed between taxonomic groups and ocean regions (Table 2, Figure 6). We therefore encourage future studies to examine potential non-linear effects, not only between demographic parameters and SST but also more generally between response classes and climate variables.

Another important consideration is that the speed of warming could potentially be more important than the absolute change in temperature. This was demonstrated

for black legged kittiwakes in the northern polar regions. Based on 36 years of monitoring and a large spatial scale (556 colonies in six different regions), the population size of study colonies only responded negatively in the case of abrupt increases in SST (Descamps et al., 2017). This could also potentially explain the apparent contradictions in the direction of SST effects on demography (e.g. in Table 2) but also suggests that the effect might be depending on the species' thermal niche (Beaugrand, 2015) and life history traits (Albouy et al., 2020).

Finally, it is worth mentioning that in our systematic review, several studies described the interaction between

other stressors and climate change, such as fisheries impacts (e.g. Munilla et al., 2007; Pardo et al., 2017; Rolland et al., 2008) or cumulative impacts (Burthe et al., 2014). Our aim in this study was to focus on climate change and variability, so we did not record these interactions or attempt to deal with synergetic effects, yet this is an important avenue for future research. Indeed, other stressors can alter or confound responses between climate and marine predators. The difficulty of estimating the vulnerability of marine predators to multiple stressors can distort our predictions of the future impact of global warming on marine predators. In this regard, the recent development of synthetic human cumulative impact variables is promising (Halpern et al., 2019; Sydeman et al., 2021).

Thermal ranges and generation time

Thermal ranges provide a valuable indicator of species' thermal niches and their vulnerability to climate change (Donelson et al., 2019, reviewed in Gvoždík, 2018). In our study, using a relatively simple approach (SST ranges extracted over species distribution ranges), we demonstrated that species with narrow thermal ranges may be more likely to be impacted by climate change (Figure 5a). Species with narrow thermal ranges mostly belonged to the families Spheniscidae, Laridae, Alcidae and Phocidae and were mainly found in polar and tropical regions (Table 1, Figure 4). The associated vulnerability of these species to climate change has been demonstrated through studies on populations of the Galapagos penguin, *Spheniscus mendiculus*, the Guanay cormorant, *Leucocarbo bougainvilliorum*, and the Peruvian booby, *Sula variegata*, that have declined in response to increasing SST (Vargas et al. 2006; Barbraud et al. 2018).

Although seabirds and marine mammals are generally long-lived species, there is a lot of variability in terms of age at first reproduction (ranging from 1 to 21 years, in studies reviewed). Studies based on species that started reproducing at a relatively old age (and thus with longer generation times, Gaillard et al., 2005) were more likely to report effects of climate change (Figure 5b). Indeed, some empirical and modelling approaches suggest that effects of climate change will be potentially amplified for higher trophic level species (Kirby & Beaugrand, 2009; Stock et al., 2014). Nonetheless, it must be noted that species with shorter generation time in our review also showed to be impacted by climate change (most proportions higher than 0.5 on Figure 5b). It is therefore possible that irrespective of differences in generation time, long-lived species like marine mammals and seabirds do not have the capacity, from an evolutionary perspective, to keep pace with the rate of environmental change currently taking place, especially for species with small

population sizes (Chevin et al., 2010; Reed et al., 2011; Sydeman et al., 2015). Further work is needed to better understand the potential differences of climate impacts on life histories (but see Richards et al., 2021).

Behavioural plasticity is likely to be more important in these species (Beever et al., 2017), enabling animals to respond to environmental changes over a shorter timescale. Such plasticity has already been demonstrated for a range of seabird and marine mammal species, and it allows them to exploit dynamic and ephemeral ocean features (e.g. Carpenter-Kling et al., 2020; Gilmour et al., 2018) even in highly variable environments (Abrahms et al., 2018). Phenotypic plasticity can potentially also buffer the impacts of climate changes through changes in anatomy, phenology and physiology (Chevin et al., 2010; Reed et al., 2011) but little is known about the effectiveness and realisation of the expression of plasticity, particularly for long generation time species (Forcada et al., 2008; Hetem et al., 2014). Ultimately, species most likely to persist in a rapidly changing environment will be those with the greatest capacity to adapt through both evolutionary changes and/or changes in phenotypic expressions (Sydeman et al., 2015). Changes in behaviour were not reported as being statistically significant for species with wide and intermediate thermal ranges, perhaps due to small sample sizes (Figure 5). In contrast, demography and behaviour showed significant climate effects for species with narrow thermal ranges (Figure 5). This confirms that behavioural plasticity may be the first 'line of defence' against rapid environmental change (Beever et al., 2017), particularly for species with narrow thermal ranges, but that these changes may rapidly extend to driving population level changes (Donelson et al., 2019). This suggests that the ability to disperse when environmental conditions become unfavourable, by migrating/shifting to other foraging or breeding areas, may be a key life history characteristic that species can use to cope with climate change. Indeed, species with a broad thermal range were less affected than other species, especially for the condition and behaviour classes (Figure 5a). However, negative effects have also been found in a variety of species with wide thermal ranges (Table 2), not only on demography but also on their ability to migrate and find suitable foraging or breeding areas (recently reviewed for cetaceans in van Weelden et al., 2021).

Other life history traits, in addition to thermal plasticity, could explain the differences between species in their adaptive responses (Sydeman et al., 2015). For example, marine predator trophic level and foraging strategy may also explain why some species do better than others under adverse environmental conditions (Sydeman et al., 2021). Therefore, future meta-analyses should ideally use a functional trait approach so that several traits can be assessed concurrently to better characterise the vulnerability of a species to climate change (see

innovative approach for cetaceans under future climatic scenarios in Albouy et al., 2020).

Coverage of response variables

Overall, observations within the demography class represented the majority of climate change observations (55%), especially for seabirds (Figure 3b), likely due to the relative ease of monitoring these colonial breeders. Our systematic review confirms that more demographic studies are needed to be able to conduct quantitative syntheses for marine top predator populations, especially for marine mammals (Table 2, Figure 6).

In contrast to seabirds, few studies investigated climate influences on marine mammal phenology (Figure 3b), despite the potential for negative consequences of ‘match-mismatch’ situations for fecundity and survival (Anderson et al., 2013; Radchuk et al., 2019; Sydeman & Bograd, 2009). This might be related to the difficulty of monitoring migration and breeding schedules in cetaceans and most pinnipeds. Indeed, only 11 studies investigated marine mammal phenology, and 7/11 were based on seals and polar bears that are land-breeding predators. In contrast, a high proportion of seabird studies reported a climate effect on phenology, consistent with other findings (Barbraud et al., 2012; Chambers et al., 2014; Sydeman et al., 2012). At a regional level, clear changes in breeding phenology have also been reported, especially in the Arctic (Descamps et al., 2019).

Despite the relative ease of monitoring the diet of land-breeding marine top predators (Hazen et al., 2019), there is a paucity of dietary observations for both marine mammals and seabirds in relation to climate change (Figure 3b). Changes in trophodynamics of marine predators may have major consequences on marine ecosystems (Hammerschlag et al., 2019) and a better understanding of dietary flexibility in relation to climate change is needed (Young et al., 2015). The few observed dietary studies we found could be related to the lack of explicit incorporation of climatic variables in predator-prey studies, where climate change is inferred rather than demonstrated to have had an influence on diet composition (e.g. Crawford et al., 2008).

Under-represented taxa and life stages

Despite the large coverage of taxonomic orders (Figure 4), the literature on climate influences on marine predators is dominated by a relatively small number of species (Table 1), due to factors such as ease of access for monitoring purposes and large breeding distributions. A broader representation of species and functional groups is essential to develop a more holistic understanding of the relationship between climate and marine biodiversity (Feeley et al., 2017). Seabirds are characterised by

a number of features that facilitate monitoring of their populations. Beyond the obvious need for terrestrial (or ice-based) nesting sites, these include the existence of a broad range of species with extensive geographic distribution, philopatry to nesting sites during and often between breeding seasons and ease of handling for ringing or attachment of tracking instruments. The much larger number of seabird-climate impact studies relative to marine mammal studies (Figure 1) is therefore not surprising and highlights the need for greater coverage of marine mammals.

Studies of juveniles (i.e. first year after independence) and immature individuals (prior to first recruitment) are also under-represented in the literature, probably because of unique difficulties in studying these age classes (Hazen et al., 2012). Juveniles and immatures may be more sensitive to environmental fluctuations (Seather et al., 2013) due to their smaller body size and inexperience, particularly with regards to foraging (Hazen et al., 2012). Non-breeding adults were also under-represented even though they often constitute a large portion of the population (Saether & Bake, 2000). They generally disperse over large areas and thus may be exposed to a greater variety of threats than while breeding. Assessments based solely on breeding individuals are likely to result in an under-estimation of the vulnerability of these populations to climate change and other anthropogenic threats (Carneiro et al., 2020; Maspons et al., 2019). Consequently, for long-lived species such as seabirds and marine mammals that face high mortality rates in these life history stages (Levitis, 2011), more studies are needed to understand and predict future population dynamics (Seather et al., 2013).

Climatic variables

The most common climate variables reported in the literature were SST (Figure S3), variables related to sea ice and global climate indices, followed by air temperature and wind and oceanographic characteristics. These variables encompass only a small part of the current and expected environmental changes according to the last IPCC report on the ocean (Bindoff et al., 2019). Moreover, some climatic changes that may directly affect marine predators at their land-based colonies, with potentially detrimental consequences on their breeding performance, have rarely been studied. For example, the potential increase in extreme weather events, including storms and heatwaves or altered precipitation patterns can directly affect seabirds (Jones et al., 2018; Oswald & Arnold, 2012; Piatt et al., 2020) and marine mammals (Castellini, 2018). The importance of these events on land-breeding predators justifies a greater focus on them in future studies assessing climate impacts on these animals (but see Oswald et al., 2008 and Sherley et al., 2012).

RECOMMENDATIONS AND CONCLUSIONS

Herein we provided a detailed overview of the literature on the effect of climate on marine mammals and seabirds. Climate change is affecting seabirds and marine mammals at different temporal and spatial scales, the nature and degree depending on the biological response studied (Figure 7). The study duration, as a function of region and response variable, proved to be critical in influencing whether observed effects on marine predators were attributed to natural climate variability or climate change (Figure 7). This is important to consider when deriving conclusions regarding the effect of climate change vs. climate variability on marine predators. A larger diversity of climatic variables should be studied, with particular focus on the under-studied changes in ocean chemical properties, heatwaves, wind regimes, storm events, and human cumulative impacts, that are expected to affect marine ecosystems (Bindoff et al., 2019; Halpern et al., 2019). There also needs to be a greater focus on dietary and physiological responses, species in the tropics and on life history stages other than breeding adults (Box 1). These are major gaps (Figure 7, Box 1) in our knowledge that should be addressed in order to better understand, predict and potentially mitigate the effects of ongoing and future climate-mediated changes on endothermic marine predators.

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AUTHORSHIP

PP and FO conceived the study with input from co-authors on the study design. FO conducted statistical analyses and together with AT extracted relevant data from research papers. With significant input from all authors, FO led the writing of the manuscript. All co-authors commented on the manuscript and approved the final version.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ele.13920>.

DATA AVAILABILITY STATEMENT

Should the manuscript be accepted, the data supporting the results will be archived on Dryad and the data DOI will be included at the end of the article (Orgeret, 2021). R codes are available upon request (<https://doi.org/10.5061/dryad.kd51c5b6v>).

ORCID

Florian Orgeret  <https://orcid.org/0000-0002-1940-7797>
 Andréa Thiebault  <https://orcid.org/0000-0001-9585-1083>
 Kit M. Kovacs  <https://orcid.org/0000-0002-5878-4819>
 Christian Lydersen  <https://orcid.org/0000-0003-3868-2345>
 Mark A. Hindell  <https://orcid.org/0000-0002-7823-7185>
 Sarah Ann Thompson  <https://orcid.org/0000-0003-1667-0853>
 William J. Sydeman  <https://orcid.org/0000-0003-1902-4654>
 Pierre A. Pistorius  <https://orcid.org/0000-0001-6561-7069>

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