What information is required to inform management decisions for migratory baleen whales in response to climate change?

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ABSTRACT

Climate change poses significant challenges for migratory baleen whales. These species rely on stable environmental conditions and prey availability in polar regions which are predicted to experience significant climate change. Predicting the impacts of climate change on whale species remains challenging due to complex interactions between environmental drivers, biological mechanisms and species-specific physiological responses to novel environmental conditions. Process-based models linking environmental drivers can elucidate causal change mechanisms, offering the most robust approach to addressing uncertainty and informing management decisions. This systematic review analysed 53 peer-reviewed studies published between 2001–2022 to assess how baleen whale responses to climate change are modelled and predicted in scientific literature, with a focus on the integration of intrinsic biological mechanisms and processes in modelling approaches. Substantial methodological and geographic biases were found, with 75% of studies focused on Northern Hemisphere populations, predominantly in the North Pacific, North Atlantic and Arctic oceans. Statistical correlative methods dominated the research landscape, with only three studies employing mechanistic approaches. Many studies (> 40%) inferred whale responses based on their knowledge or assumptions, rather than explicitly testing responses via biological mechanisms. While the majority of studies reported negative responses to climate drivers, some species demonstrated potential adaptability through range shifts and prey switching. Significant knowledge gaps were identified, including limited physiological research, minimal studies on Southern Hemisphere populations and few investigations of complex environmental interactions. The review highlights the critical need for process-based models incorporating physiological mechanisms, species-specific characteristics and comprehensive environmental data to develop robust predictions and management strategies.

KEYWORDS: CLIMATE CHANGE; TRENDS; CONSERVATION; MODELLING; FEEDING GROUNDS; MIGRATION; PHYSIOLOGY; FOOD/PREY

INTRODUCTION

Global warming and changes in climatic conditions are affecting ocean environments worldwide. Polar regions are experiencing accelerated changes, with warming oceans, melting sea-ice, warming oceans, increasing acidity, and changes to ocean circulation and stratification affecting primary productivity and linked food chains (Meredith *et al*., 2019; IPCC, 2022). Species that depend on stable conditions in polar regions, such as migratory baleen whales, may be especially susceptible to changes in ocean environments (Laidre *et al*., 2008), particularly

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those populations still recovering from historical commercial whaling (Tulloch *et al*., 2018, 2019). The vast spatiotemporal scale(s) of ocean climate change, occurring across entire ocean basins and over decades, creates significant challenges for understanding and predicting impacts on baleen whales, whose biological imperatives of feeding, breeding and migration operate on more constrained seasonal and regional schedules (Fig. 1). Responses to change are challenging to predict, due to the potential mismatch in drivers versus responses, and because species respond to change in complex ways, for example with local adaptation and phenotypic plasticity, but also with non-linear responses in species-environment relationships that could trigger species declines (Derville *et al*., 2019; Tulloch *et al*., 2019; Meynecke *et al*., 2020). Because of this, our understanding of potential climate-driven impacts on long-lived baleen whale species, and how to manage future change, is still limited.

Discussion of climate change at the International Whaling Commission's (IWC) Scientific Committee began in 1995 with the first workshop on climate change (IWC, 2007). Four further IWC workshops followed (IWC, 2010, 2012, 2022; Nunny & Simmonds, 2020), with recommendations endorsed by the Commission in 2009 to expand its work on climate change impacts on cetaceans. In 2022, the Commission established the Intersessional Group on Climate Change (IGC) to assess the latest information on cetacean populations, provide advice on tools to mitigate its impact, build resilience and develop an IWC climate change response programme. A series of further recommendations made by the IGC have been endorsed by the IWC Scientific Committee (IWC68), including improving methods to distinguish climate-related impacts on cetacean responses to better interpret current and future changes, and develop best practice guidance for future studies (Simmonds, 2024).

Predictive models can help managers anticipate the impacts of climate change on future properties of marine species and inform management decisions (Mouquet *et al*., 2015). Many approaches exist for modelling and predicting the responses of natural ecosystems and species to change, each with their own merits and drawbacks. The precision of ecological predictions ranges from 'hunches', based on expert opinion or rules of thumb, to extrapolation, based on observed statistical relationships, to process-based approaches and complex simulation models, based on long-term empirical data (Cuddington *et al*., 2013) (Table S1). Each framework differs in its capacity to support management decisions within the context of global change. Expert opinion has the advantage of allowing rapid response given limited data and resources, but its appropriateness for future projections is limited due to assumptions and high uncertainty. Statistical extrapolations require relatively minimal data, and are typically correlative in nature, enabling rapid assessment of combinations of biotic (e.g., species range) and abiotic (e.g., temperature and climate patterns) variables. The peer-reviewed literature increasingly recommends the use of dynamic process-based models (Box A) grounded in ecological theory to guide future management decisions, which include both extrinsic environmental conditions as well as underlying intrinsic biological mechanisms or processes (Davis *et al*., 1998; Urban *et al*., 2016; Guillaumot *et al*., 2022; Tourinho & Vale, 2023). But how often are these methods used in research to understand the responses of baleen whales to climate change? Where are the gaps that need to be filled to manage vulnerable populations given these changes in their ocean environments?

Process-based models (also called 'mechanistic models') are based on explicit assumptions about how systems or species work, grounded in ecological theory (Box A, Table S1). Combining intrinsic biological characteristics or processes (e.g., physiology, evolution, demographic shifts, migratory phenology, population dynamics (Berg *et al*., 2010; Bellard *et al*., 2012; Urban *et al*., 2016) with extrinsic environmental factors (e.g., climate, oceanography, bathymetry (Williams *et al*., 2008)) has been shown to better inform species trends and responses to changes in their environment (Mouquet *et al*., 2015; Urban *et al*., 2016). Such models, however, typically require more time and resources to develop, as well as needing high-quality empirical data about how a species' unique biology governs its responses to climate (Williams *et al*., 2008; Hof, 2021). Because process-based approaches are based on causal mechanisms, they are better suited to future extrapolation beyond known conditions than correlative methods (Cuddington *et al*., 2013) (Table S1). Correlative methods are informed by present or past conditions of a system (e.g., niche-based species distribution models such as MaxEnt (Phillips *et al*., 2006). However, future environments will involve unique combinations of biotic and abiotic variables, different from anything known previously. Models using correlative methods that extrapolate beyond known data to such novel or unique conditions may be unreliable (Cuddington *et al*., 2013), given that these abiotic variables will likely fall outside the range of parameters used to construct the model (Elith *et al*., 2010; Kearney *et al*., 2010).

Because of this, many argue correlative methods have poor predictive power (Evans *et al*., 2015). Correlative methods that do not include mechanistically-linked attributes of the system cannot be used to quantify cause-effect relationships and may even produce false predictions based on spurious correlations in the data, missing collinear variables, or indirect effects not accounted for in the model (Kearney & Porter, 2009; Evans *et al*., 2015). Because of this, such models have limited practical value for environmental management (Schuwirth *et al*., 2019).

Box A. Process-based models

Process-based (or mechanistic) models are mathematical representations of a system that explicitly describe the key biological and physical processes that drive ecosystem dynamics using mathematical equations. They incorporate direct cause-and-effect relationships, such as how environmental conditions affect physiological rates, energy budgets and population dynamics. For baleen whales, these models might include equations describing how ocean temperature and prey availability influence metabolic costs, foraging success, competition, predation rates, reproductive rates and, ultimately, population growth. For example, Tulloch *et al*. (2019) use mathematical equations to link key climate processes (sea-surface temperature driven by climate change) to krill growth and abundance, and changing whale population abundances, through key biological processes including predation and competition. In doing so, they robustly predict how reduced prey availability in traditional feeding grounds could lead to population declines. This mechanistic understanding is particularly valuable for long-lived species like baleen whales, where historical correlations may not hold as climate change creates unprecedented environmental conditions.

More complex predictive models can include combinations of rule-based, statistical and process-based components at individual species or ecosystem scales (Carpenter, 2003; Cuddington *et al*., 2013). Unlike correlative models that only capture statistical relationships, these models allow us to understand and predict how multiple interacting mechanisms – e.g., changes in prey distribution, ocean acidification impacts on prey species and shifting migration patterns – collectively affect whale populations under novel climate conditions. Ecosystem models and simulation models have the advantage of being grounded in ecological theory but typically require a larger number of parameters and functions than other models that can increase uncertainty in model predictions (Fulton *et al*., 2003). Management decisions for marine species and stocks are increasingly informed by multi-species ecosystem models that incorporate mechanistic components (Plagányi, 2007; Smith *et al*., 2007; Travers *et al*., 2007; Hobday, 2010; Plagányi *et al*., 2011; Pethybridge *et al*., 2020). Because these models are rigorous, include intrinsic processes and interactions, and are usually fitted to data, they are well-suited for guiding decisions in a climate-change context, although examples for cetaceans are still rare (Plagányi & Butterworth, 2012; Tulloch *et al*., 2019). Complex models that include interactions between humans, species and other biophysical components, such as large-scale end-to-end models (Smith *et al*., 2007; Travers *et al*., 2007), are also suited to capturing the multifaceted spatial and temporal scales at which key processes operate relevant for understanding migratory whale responses to climate change (Fig. 1). Such models are often developed at relatively large scales, which may in part address mismatches between the spatial and temporal scales of physical versus ecological processes (Fulton *et al*., 2019).

An increasing number of review papers and meta-analyses have accumulated over recent decades describing the susceptibility of cetaceans to climate change, using qualitative methods (Simmonds & Isaac, 2007; Laidre *et al*., 2008; Moore & Huntington, 2008; Simmonds & Eliott, 2009; Nunny & Simmonds, 2020), or quantitative analyses (Learmonth *et al*., 2006; van Weelden *et al*., 2021). The endeavours to date provide valuable information on the current state of many cetacean species and populations, although data is lacking for many species. Climate change impacts on whales may be direct, for example changes in water temperature causing physiological stress, or indirect, such as changes in prey availability or habitat suitability (Learmonth *et al*., 2006), which, in turn, may affect emergent properties of whale populations, such as abundance and distribution (Urban *et al*., 2016; Nunny & Simmonds, 2020; van Weelden *et al*., 2021). Despite ongoing recommendations for the use of process-based

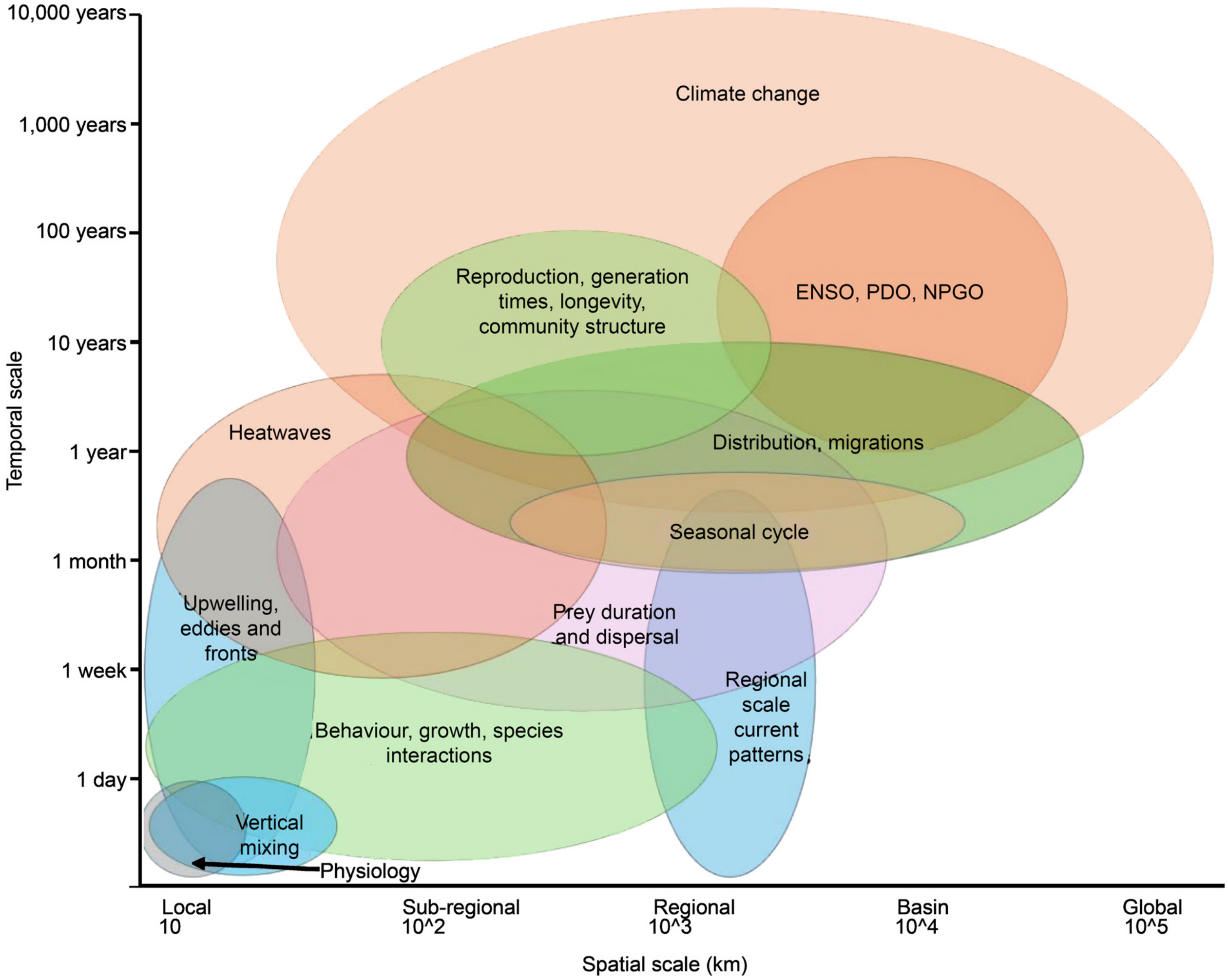

Figure 1. Spatial and temporal scales of climate (orange) and oceanic or other environmental-driven processes (blue), compared with the spatial and temporal scales of key ecological, biological and demographic factors for baleen whales (green) and their prey (purple) Redrawn and adapted from Carr *et al*. (2011).

models that explicitly include biological mechanisms to adequately understand and manage species in a changing world, there has been no evaluation of the suitability and effectiveness of model choices to predict vulnerability or susceptibility of baleen whales to climate change.

To address these knowledge gaps, a systematic review of the literature from past decades was conducted, with the aim of studying and predicting responses of migratory baleen whales to climate change. The methodologies were assessed to examine the study design, models, data and variables, and to assess whether biological mechanisms or intrinsic processes were included in the model. The results identify where gaps in the literature exist for baleen whale species globally, at a species level, spatially and methodologically. A discussion follows to highlight the utility of appropriate models to inform management decisions, based on the type of model and analyses used in the study. Finally, recommendations for future scientific research are provided to guide monitoring and experimental efforts aimed at informing current and future responses of baleen whales to climate change.

METHODS

Literature review

To assess the types of information and models employed to date in the climate change response literature for baleen whales, a quantitative literature review and bibliographic analyses were conducted. The literature review was carried out according to the Systematic Literature Review (SLR) method described by Siddaway *et al*. (2019),

Table 1
Search terms used in the literature review.

Factor	Exact search term	Representing
Included in all searches		
Climate change	Topic or Title = ((climat* AND (chang* OR warm*)) OR (temperature* AND (increas* OR ris* OR warm*)))	Climate change
Family	Topic or Title = (cetacea* OR whale* or dolphin* OR porpoise* OR narwhal* or beluga*)	Cetacean species
Included in the baleen whale search		
Species	All fields = ((blue whale*) OR (humpback whale*) OR (right whale*) OR (fin whale*) OR (sei whale*) OR (bowhead whale*) OR (minke whale*) OR (gray whale*) OR (grey whale*))	Antarctic minke whale *(Balaenoptera bonaerensis)* Blue whale *(Balaenoptera musculus)* Pygmy blue whale (*Balaenoptera musculus brevicauda)* Bowhead whale *(Balaena mysticetus)* Dwarf minke whale (*Balaenoptera acutorostrata subsp*.) Common minke whale *(Balaenoptera acutorostrata)* Fin whale *(Balaenoptera physalus)* Grey whale *(Eschrichtius robustus)* Humpback whale *(Megaptera novaeangliae)* North Atlantic right whale *(Eubalaena glacialis)* North Pacific right whale *(Eubalaena japonica)* Southern right whale *(Eubalaena australis)* Sei whale *(Balaenoptera borealis)*

using the Preferred Reporting Items for Systematic Reviews and MetaAnalyses (PRISMA) checklist and flowchart (Moher *et al*., 2015). The search was carried out on the Clarivate Web of Science database[3] applying different combinations of search terms (Table 1) to quantify the number of published studies and analyse information on those studies. The terms were combined as title searches ('TI' in the advanced search of the Web of Science core collection) or topic searches ('TS') to vary the level of emphasis on different factors. An initial search for all cetacean species was conducted for comparative purposes. The search was then restricted to baleen whale species that migrate to or rely heavily on polar regions only using a search term containing species names (Table 1). Whales that are not fully migratory and remain in tropical or temperate waters (Bryde's whale (*Balaenoptera brydei*), Omura's whale (*Balaenoptera omurai*), Rice's whale (*Balaenoptera ricei*), Eden's whale (*Balaenoptera edeni*), pygmy right whale (*Caperea marginata*)) were excluded due to their non-reliance on polar regions and associated prey availability where predicted high environmental change is expected. As the overall focus was on research in an explicit climate change context on baleen whales, climate change search terms (Table 1) were held constant (either as title or topic search). The search string was run with a cut-off date of 2 July 2022.

Screening and eligibility

Non-peer-reviewed articles were excluded. Articles not written in English were also excluded (Fig. S1). Subsequently, papers were excluded if not deemed relevant following a screening of the titles and abstracts if they were not focused on climate change, or if the chosen baleen whale species was not one of those indicated in Table 1. This was followed by an eligibility assessment based on the full text. Papers were excluded if they met one or more of the following criteria:

- not directly related to climate change;
- review with no primary data and/or speculative;
- had a study period of < 3 years;
- focused on theoretical concepts only (e.g., developing a new method or concept) versus analysing primary data.

For the included papers, information on the following components were recorded: focal species, geographical region, method and model used (if any), environmental variables affected by climate change specifically in

[3] *https://apps.webofknowledge.com*

polar regions (sea-ice extent/thickness/volume, sea-surface temperature (SST), ocean acidification/dissolved pH, circulation, salinity, chlorophyll (Chl_a), mixed layer depth/stratification, (IPCC, 2022)) and key findings. For geographical region, 'Arctic' was used for areas inside the Arctic Circle and also the areas adjacent to the Arctic Circle where endemic whales are present, e.g., Greenland. 'Antarctic' was used for studies focused on areas within the Southern Ocean. Other region categories were derived by ocean basin and region: 'Atlantic Ocean (North)', 'Atlantic Ocean (South)', 'Pacific Ocean (North)', 'Pacific Ocean (South)', 'Indian Ocean'. The category 'Worldwide' was used for papers that covered multiple regions or discussed global trends rather than focusing on specific regions.

Methods were assigned to four broad categories: (1) expert opinion/qualitative assessment; (2) extrapolation (by statistical, correlative or empirical methodology); (3) process-based or mechanistic; and (4) simulation. The following information from each study was recorded: model type (if any) used in the analysis; whether the study was experimental (based on historical data) or predictive; the response variable (i.e., evaluating distribution/range, abundance, evolutionary traits/genetics, foraging ecology, population dynamics, phenology), and biological response mechanisms, categorised into five main classes, derived from Urban *et al*. (2016) ((1) physiology; (2) demography, life history and phenology; (3) evolutionary potential, selection and population differentiation; (4) species interactions; and (5) dispersal and range dynamics) to which each study attributed a species' response to climate change (Table S2); and whether these mechanisms were tested explicitly (e.g., through a model or statistical method) or inferred by the authors from their knowledge of their study system (in a qualitative manner after results were obtained). To assess the level of integration of biological mechanisms in the climate change response literature for baleen whales, an in-depth search of the results of the literature review was conducted to determine which papers included a physiological focus (e.g., investigating metabolic rates/adaptation/limits, physiological rates, thermal tolerances, phenotypic plasticity).

RESULTS

General overview

The initial literature search focused on all cetaceans and climate change identified 1,050 papers, with the number increasing exponentially since 1998 (Fig. 2A). Less than one quarter of these focused on baleen whale species (n = 242), with the majority published in the last 10 years (Fig. 2A). Screening and eligibility assessment of these papers returned only 53 studies relevant to climate change response, for 10 species (Fig. 2B). Although the studies were conducted in 20 countries, the literature was geographically biased, with most studies occurring in the

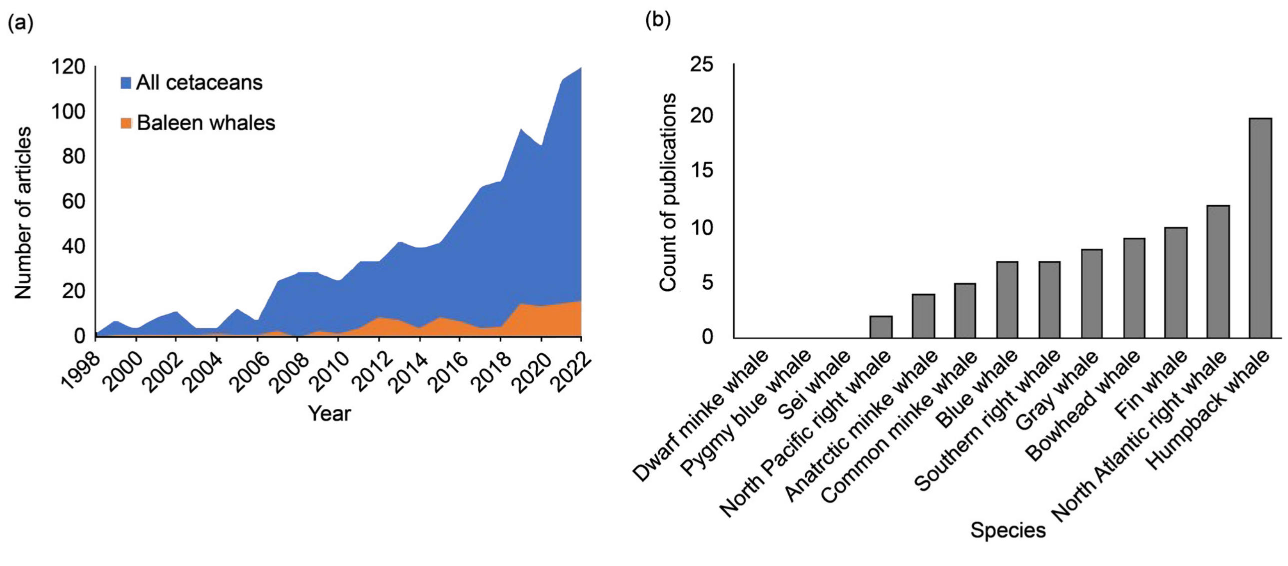

Figure 2. (A) Number of studies in the literature review published per year for all cetaceans (total 1,050) and just baleen whales (total 242). Different coloured bands are cumulative within years, such that a thicker band represents more studies published in a single year. (B) Number of instances a species occurs in the studies in the dataset included in the systematic review (n = 53).

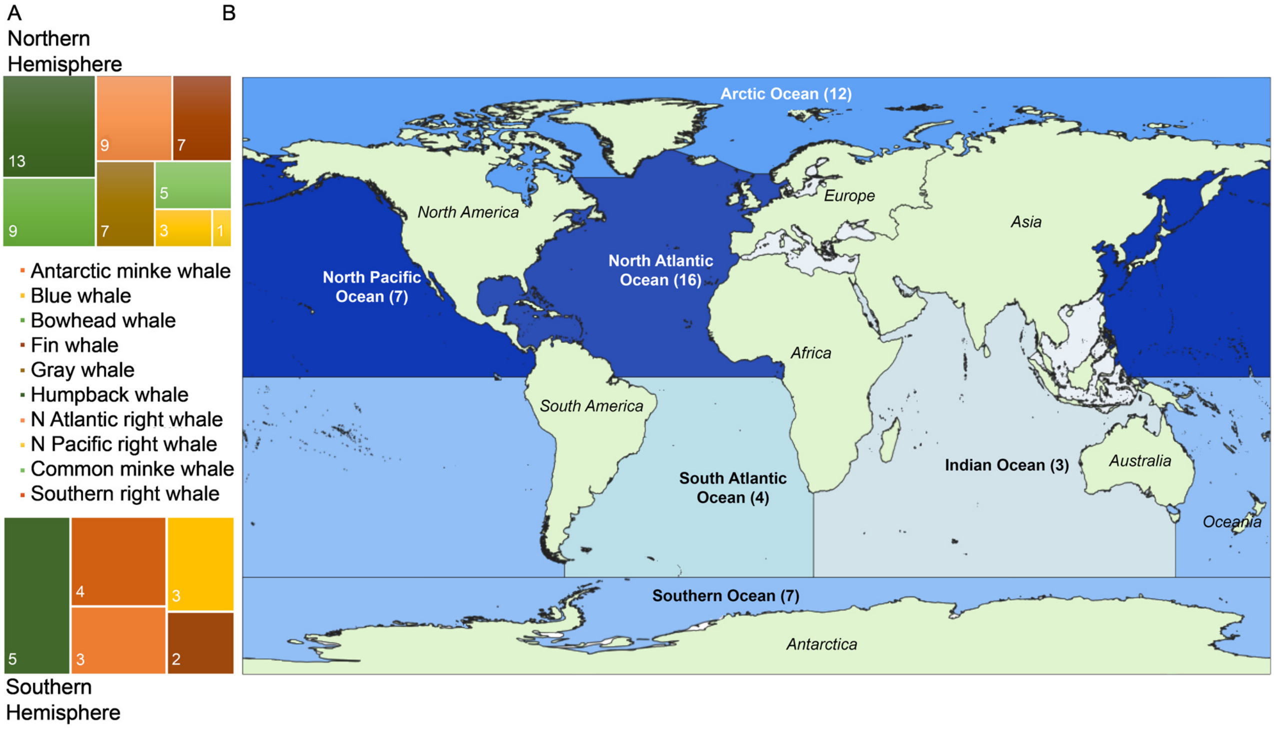

Figure 3. (A) Number of studies focused on each searched baleen whale species shown as a treemap (size of each box proportional to the number of studies for each species). (B) Map of global oceans and seas, identifying the number of studies included in the refined literature review. Darkest blue identifies the highest numbers of studies in that region; light blue identifies lowest number of studies (total numbers for each region displayed in the label). Boundaries from the Flanders Marine Data Centre.

Northern Hemisphere (75%), in the North Pacific, North Atlantic and Arctic oceans (29%, 27% and 21% respectively), and the least in the Indian ocean and South Atlantic ocean (6% and 4% respectively; Fig. 3). Similarly, Northern Hemisphere species or populations of baleen whales were the most frequently studied, with 23% of papers focused on northern populations of humpback whales (*M. novaeangliae*) (and only 13% focused on southern populations), 21% on North Atlantic right whales, and 16% on bowhead whales (Figs. 2B, 3). Only 4% of studies focused on the North Pacific right whale, with no relevant papers on pygmy blue, dwarf minke or sei whales (Fig. 2B).

Most studies (n = 38) were based on regional areas (small seas and state or provincial coastal regions) ranging from ~20,000 km^2 to ~900,000 km^2, with 25% of all studies focused spatially on areas < 10,000 km^2. In five cases, the study was focused on highly localised regions < 5,000 km^2. The temporal extent of studies ranged from three years (2012–14) to 308 years (1890–2100) (Fig. 4). Studies largely focused on historical or recent time periods from 1985 to 2020, with only eight studies predicting responses into the future. Although studies using predictive models were based across large temporal (> 50 years) and spatial extents (basin to hemisphere scale), there were instances of ocean-scale studies with < 5 years of data, and many models based on regional areas had relatively small temporal extents (< 10 years, Fig. 4).

Environmental and climate data in models

Recent advancements in technology have facilitated access to increasing amounts of environmental data, sourced from remote sensing with enhanced spatial resolutions, interpolation of data, and modelling techniques, such as those used in various climate data products (Melo-Merino *et al*., 2020). Four main sources of environmental information were used: (1) global databases or repositories providing climate and other environmental parameters for whole oceans; (2) regional databases; (3) data collected by the authors through either field measurements or computational methods (n = 6); and (4) published information. The most common (n = 38) were global databases, including the National Aeronautics and Space Administration (NASA) and National Oceanic and Atmospheric Administration (NOAA). Other data included Ocean Color Web, Ocean Colour Climate Change

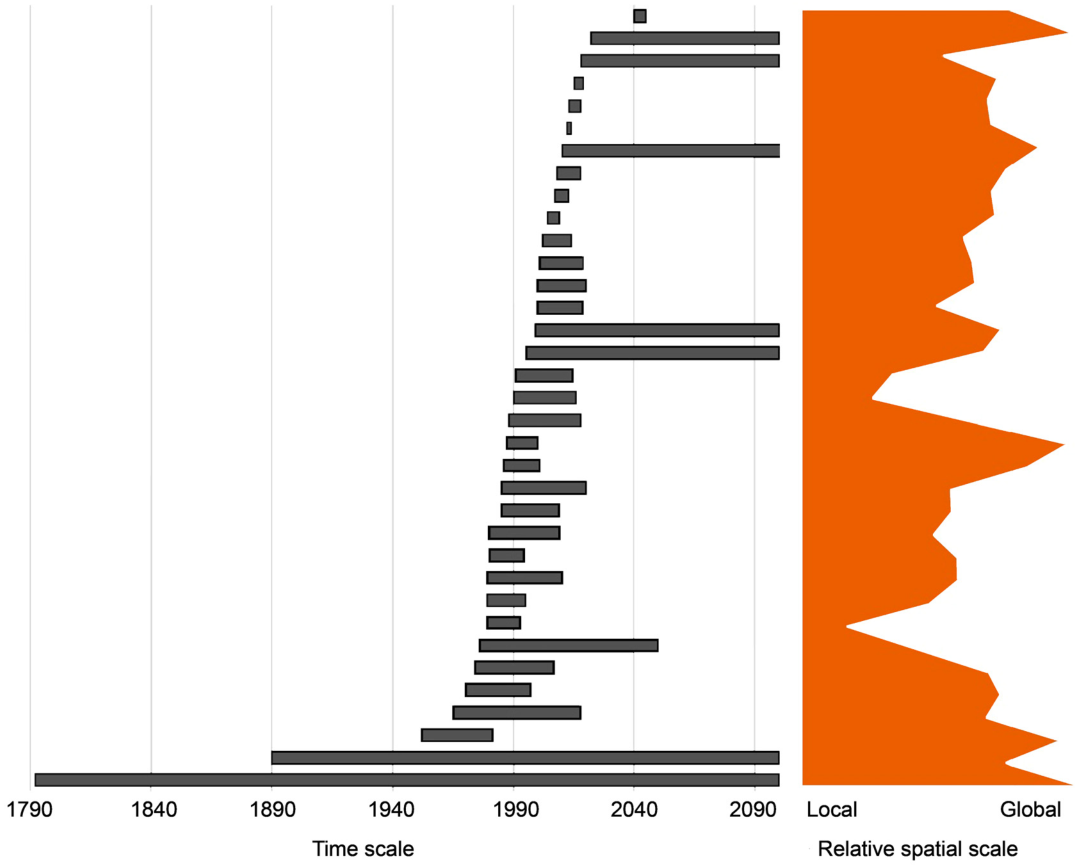

Figure 4. Comparison of time scale for studies included in the review vs. their relative spatial scale (study area (log-transformed km^2), with peaks representing global or other large-scale studies, and troughs representing local-scale studies with the smallest area (log-transformed km^2)).

Initiative, Australia Community Climate and Earths System Simulator (ACCESS; (Ziehn *et al*., 2017), Coupled Model Intercomparison Project models (CMIP5; Taylor *et al*., 2012), The Copernicus Marine Environment Monitoring Service (CMEMS), AquaMaps, World Ocean Atlas (WOA), and the International Comprehensive Ocean-Atmosphere Data Set (ICOADS). Regional databases included local information from NOAA CoastWatch website, Arctic Data archive System, Canadian Ice Service digital ice chart; and Regional Ocean Modeling System (ROMS). Local field measurements (SST, salinity, Chl_a) were collected for validation or statistical correlation in six studies. The most cited source for bathymetric data was the General Bathymetric Chart of the Oceans (GEBCO), which offers a 15 arc-second resolution grid for the global ocean (Melo-Merino *et al*., 2020), and was used as input for 12 studies, 10 of which were correlative SDMs.

Three-quarters of studies (n = 39) evaluated baleen whale responses to changing SST, although only 28 of these explicitly linked SST changes to whale responses in their models or analyses (Fig. S2). Sea-ice was the second most common environmental variable included (n = 18), though only half of these explicitly linked sea-ice change to whale response (Fig. S2). No studies evaluated changing ocean pH, and few evaluated mixed layer depth or salinity changes (n = 3 and n = 5 instances respectively). Chlorophyll data were included in 12 analyses, most often as a proxy for other plankton prey, with three studies linking these data to krill. Almost half of the studies (n = 25) incorporated more than one environmental variable, with SST included in all these studies, and 11 studies including sea-ice change and SST. Only nine studies included more than two climate change-related environmental variables. In seven instances, climate change was inferred (through temporal change) or assumed (via warming or changes in prey), but explicit environmental data were not included in the analysis. Over 25% (n = 14) of the studies evaluated identified regional modes of climate variability (e.g., Pacific Decadal Oscillation (PDO), Atlantic Multi-decadal Oscillation (AMO), North Pacific Gyre Oscillation (NPGO) and El Niño-Southern Oscillation (ENSO)) as likely drivers of change.

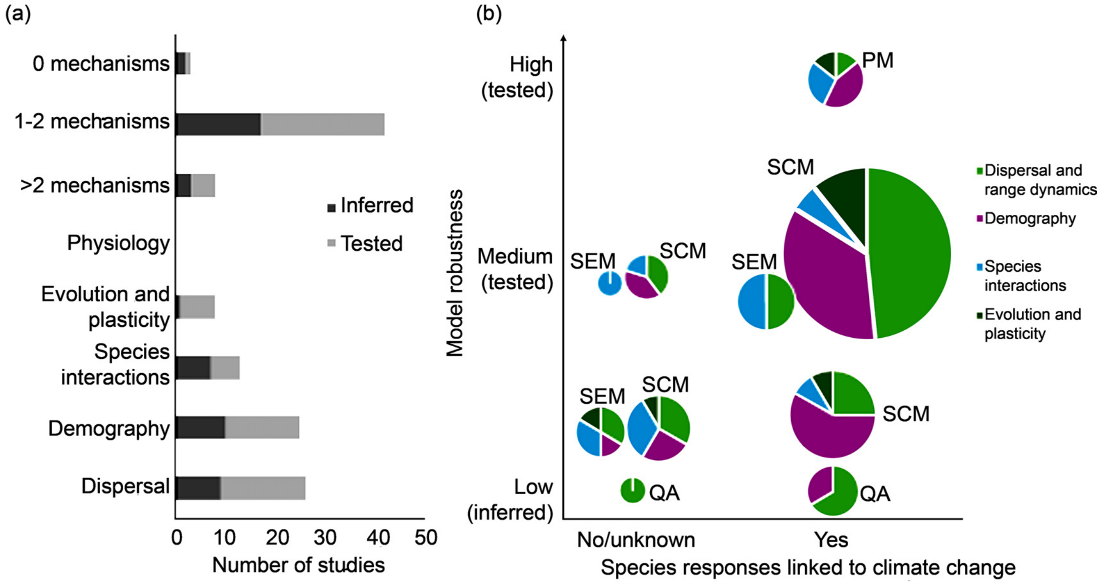

Figure 5. Comparison of biological mechanisms studies, highlighting (A) the total number of studies within each mechanism category (see Table S2), split by inferred or tested findings. Over one third of studies inferred findings vs. testing. (B) The model's explanatory power and robustness is shown on the y-axis (from low robustness due to inferred information, such as qualitative assessment (QA), to moderate robustness from statistical inference or testing (SEM = statistical explanatory model, SCM = statistical correlative model), to high robustness from process-based models (PM that include mechanistic linkages), compared with whether the authors identified climate change as the primary driver of species responses on the x-axis.

Experimental methods and biological mechanisms

The most common experimental design was statistical extrapolation (n = 46), with > 40% of these studies inferring findings versus explicitly testing the response mechanisms (Fig. S2). Almost two-thirds of all studies (n = 31) used correlative statistical methods (e.g., species distribution models, such as MaxEnt (Buckley *et al*., 2011; Elith *et al*., 2011), simple regression-based methods, such as generalised linear models (McCullagh, 2019), and generalised additive models (Hastie, 2017)), while the remainder used descriptive analytics (e.g., frequency distribution and extrapolation). There were only two instances of process-based models (using dynamic population models) that explicitly tested and predicted physiological responses to climate change (adult survival, calf survival) (Fig. S2) (Meyer-Gutbrod *et al*., 2015; Agrelo *et al*., 2021). Only one study used a complex simulation model that explicitly tested several biological response mechanisms to climate change including competition, mortality and foraging dynamics (Tulloch *et al*., 2019).

The majority of studies tested 1–2 mechanisms (n = 42). No model included all five biological mechanisms (from Table S2), only eight included > 2 mechanisms, and no model tested physiological responses (Fig. 5A). Responses of baleen whales to environmental variables were inferred rather than tested in almost half (n = 23) of the 53 studies. Dispersal mechanisms (distribution, range shifts, range expansion/contraction) and demographic or phenological mechanisms (assessments of abundance and population growth/decline, reproductive success, survival/mortality, breeding success/calving rates (Fig. S4)) were the most commonly studied (n = 27 and n = 25 respectively), although one-third of these inferred their findings versus explicitly testing mechanisms (Fig. 5). Ten papers studied both distribution and abundance responses. Of the 14 studies evaluating interactions (diet/foraging dynamics, predation, competition and evolution), half inferred responses versus explicitly testing responses. Indirect responses to climate change (i.e., prey-mediated) were evaluated in 10 papers. The most common prey type included in models or evaluated alongside whale responses was euphausiids (n = 8), followed by copepods (n = 7). Three studies based in the northern hemisphere also evaluated responses of whales to climate change in association with fish species (capelin, sand eel, sardines). Studies testing evolutionary responses were rare (only two).

Summary of responses across species

More studies reported negative responses of baleen whales to climate drivers and/or environmental variables (n = 20) than positive (n = 13), with almost half reporting neutral, inconclusive or no response(s). For eight of the 13 baleen whale species, a mix of positive and negative observed and/or predicted effects were reported, depending on the response mechanism evaluated in the study (Fig. 6). Exceptions to this were fin whales, common minke whales and North Atlantic right whales, for which relevant studies found only negative or neutral responses. In the Southern Hemisphere, largely negative responses are predicted for baleen whales in response

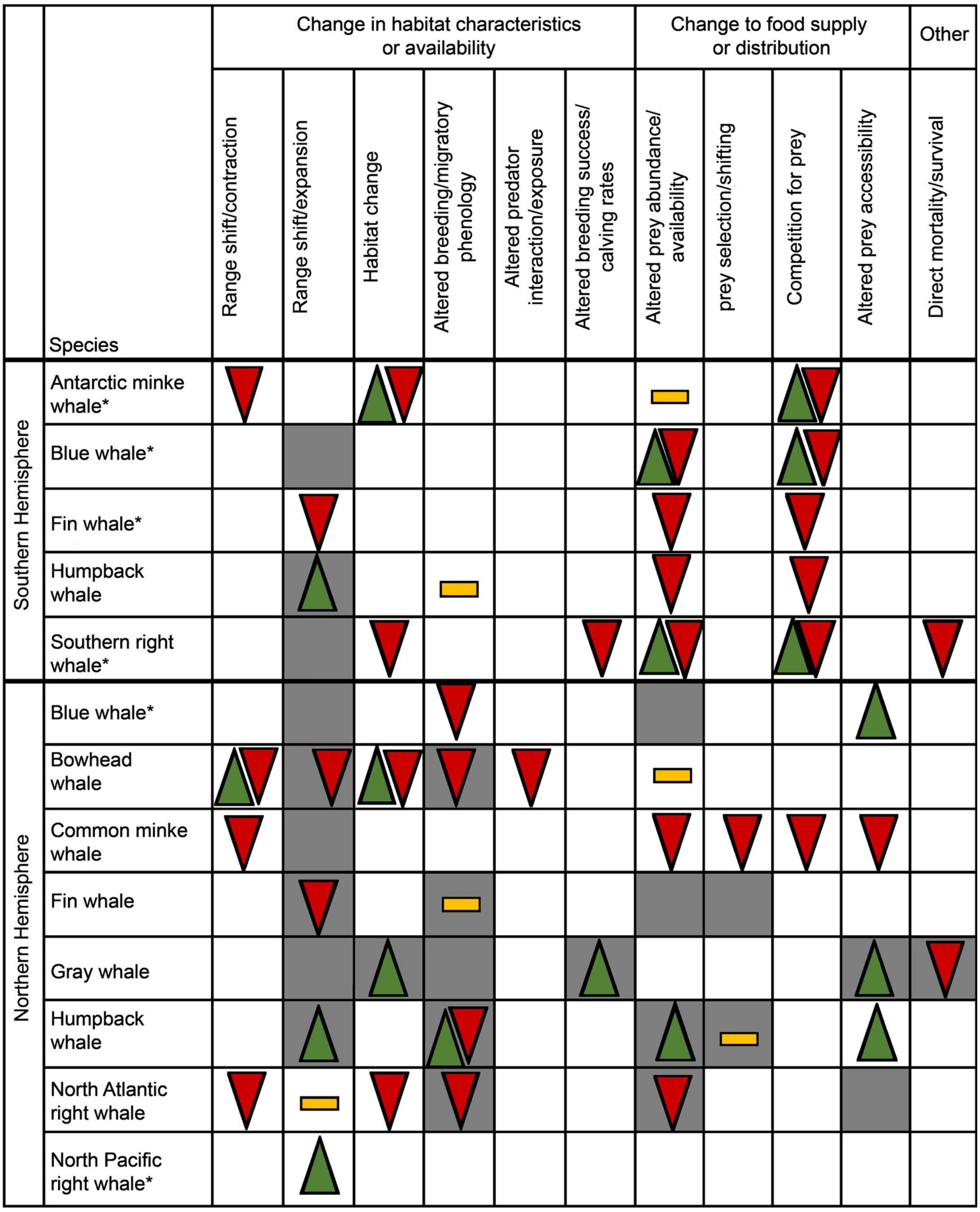

Figure 6. Type of climate change effect (change in habitat characteristics or availability, or change to food supply or distribution), and direction of impact for whale populations in the Southern Hemisphere, and Northern Hemisphere, derived from studies that explicitly link climate change variable to responses (arrow up = positive, arrow down = negative, dash = neutral or no change, two arrows = possible spatial differences in response). Grey shading indicates uncertain response (due to deficiencies in matching cause-effect relationships through analytical methods from the review), or inconclusive findings across studies. *indicates three or fewer studies. References provided in Table S3.

to changes in food availability, although mix of positive and negative responses are predicted for Southern right whales, blue whales and Antarctic minke whales, largely due to reported spatial heterogeneity in the intensity of environmental change in the Southern Ocean. Spatial differences between ocean basins were found in Southern Hemisphere population responses for blue, humpback and Southern right whale populations (Fig. 6), but these were based on a small sample of studies (n = 2). Studies yielding ambiguous or inconclusive results were based largely in the Northern Hemisphere and used correlative statistical methods (n = 19). Fourteen of these studies documented northern distribution shifts and possible range expansions for whale populations but could not conclusively assess the ecological implications of these movements (Fig. 6). Similarly, fin and gray whale responses to change in habitat or prey availability were largely inconclusive (Fig. 6).

Among the 30 papers explicitly examining baleen whale climate responses (versus inferring results), studies predominantly focused on food supply and distribution changes, with notably higher uncertainty in assessing habitat characteristics and availability under climate change (Fig. 6). Substantially more studies focused on Northern Hemisphere populations and species (n = 27), except for those focused on North Pacific right whales. Only one mechanistic study explicitly tested range changes to changing environmental conditions (Zerbini *et al*., 2015).

DISCUSSION

Consideration of both extrinsic environmental conditions and fundamental biological or physiological mechanisms are needed in concert with mechanistic modelling approaches for accurate future forecasting (Hof, 2021; Williams *et al*., 2008). This systematic review of migratory baleen whale responses to climate change, however, found only three studies using mechanistic approaches, with the majority using statistical correlative or extrapolative methods. Other substantial gaps and biases in the scientific literature were found, from species studied and the location of research, to whale biological responses to change. The strong species and geographic research biases limit inferences for managing baleen whale species in many regions. Most studies to date focus on whale populations in the North Pacific, North Atlantic and Arctic oceans (Fig. 3). Comparatively little is known about baleen whale responses to environmental change in the Southern Hemisphere. The geographic trends found may simply reflect locations where climate change impacts are expected to be most intense (e.g., Arctic region), or could reflect a focus on species that are highly vulnerable and are currently at low abundances, or are decreasing in abundance (e.g., North Atlantic right whale). Very few studies focused on the critically endangered North Pacific right whale, with no studies at all focused on the sei whale, a species listed as endangered by the IUCN Red List. The geographic bias is more likely an artefact of the detectability of baleen whales off the coast of North America and relative ease of monitoring and availability of resources and funding for such research (Knowlton *et al*., 2012), compared to the challenges of surveying whales in the Southern Ocean (Williams *et al*., 2014). The lack of studies focused on southern regions is troubling, especially given that most Southern Hemisphere species of baleen whales were pushed to the brink of extinction by historic commercial whaling (Clapham, 2002), with many populations yet to recover (Tulloch *et al*., 2018, 2019). Very high-resolution satellite imagery is one proposed solution for monitoring remote, high-latitude oceans and associated marine megafauna (Höschle *et al*., 2021; LaRue *et al*., 2022). This fast-advancing technology is able to help detect and monitor baleen whales, although its ability to differentiate species and inform abundance is currently limited as a standalone monitoring program. Multi-model solutions are recommended (e.g., combining satellite imagery with traditional survey methods). Future work in this discipline focused on southern populations of humpback whales, fin whales, blue whales, Antarctic minke whales and Southern right whales could do much to fill these gaps in our knowledge.

While the number of models evaluating climate change impacts on species is increasing, biological responses remain difficult to predict, due to limited research into fundamental mechanisms like physiological adaptations, species interactions and evolutionary responses (Davis *et al*., 1998; Urban *et al*., 2016). The dominant methodologies found in this review were statistical correlative approaches (e.g., SDMs and statistical regressions) that were unable to include biological mechanisms. This is problematic given the consensus that models ignoring biological mechanisms are unreliable (Norberg *et al*., 2012; Urban *et al*., 2016; Zurell *et al*., 2016). Basing decisions on such models may increase the risk of policy or management failures (Dawson *et al*., 2011), especially those that extrapolate correlations between current species' ranges and climate. SDM predictions of responses to recent climate change have been shown to improve by including species-specific physiology (Buckley *et al*., 2011) but more detailed mechanistic models can better account for interspecific physiological differences. To make informed decisions about the future, it is crucial to consider the robustness of approaches to changing conditions that may be outside the scope of past conditions (Williams *et al*., 2007). This reinforces the need for future-focused, process-based research that explicitly incorporates information on physiology and species characteristics to better understand the responses of baleen whales to climate change.

Despite prevalent negative responses of baleen whales to climate change found in this review, some species demonstrated potential adaptability through range shifts, migration timing adjustments and prey switching strategies, suggesting varied resilience to a changing climate (Fig. 6). Researchers agree that behavioural flexibility and dispersal are likely the primary mechanisms enabling whale species to adapt to climate-induced environmental changes (Fortune *et al*., 2023). However, this review found cause-effect relationships were highly uncertain or not able to be quantified based on experimental methods for a wide variety of climate conditions and associated response variables. For many Northern Hemisphere populations and/or species, findings were inconclusive. Difficulties in determining a conclusive response to specific environmental change may lie in the methodology used, with the majority using correlative statistical approaches. Causative findings are attainable using process-based methods that model relevant biological mechanisms (Shipley, 1999; Cuddington *et al*., 2013). More than 40% of the studies reviewed here relied on inference or subjective opinion, versus explicitly testing whale responses to environmental variables (Fig. 5). Physiological responses of baleen whales to climate change were tested in only a handful of papers (Fig. 5). This paper does not aim to criticise the existing literature on baleen whale responses to climate change: we note recent reviews that discuss some of the whale distribution changes in more detail (Nunny & Simmonds, 2020; van Weelden *et al*., 2021). In addition to these valuable contributions, additional mechanistic studies may be needed to ensure that conclusions drawn about species' responses to climate change are robust and well-supported.

There may be various reasons for the large gap between mechanistic and correlative research. Process-based methods and models are inherently more complex and difficult to develop, requiring more time, resources and often more data (Ruiz-Benito *et al*., 2020). One of the main factors inhibiting the incorporation of physiological information for large whales that migrate across vast distances may relate to differences in data availability, methodological approaches, and, consequently, spatial scope. The lack of viable methods for non-lethal capture to obtain blood samples from these species hinders the application of classic physiology tools, although recent advancements in nonlethal and noninvasive sampling techniques make it possible to study even the largest whale species (e.g., sampling feces, respiratory vapor, skin and blubber biopsies, and visual health assessments (Bradford *et al*., 2012; Hunt *et al*., 2015). By integrating environmental and physiological data with whale abundance and distribution data collected at large spatial and/or temporal scales, one can construct an understanding of physiological responses to long-term disturbances (Rolland *et al*., 2012; Hunt *et al*., 2015).

The temporal and spatial scales of global warming and associated marine environmental change are vast, acting at basin to ocean to global scales (Fig. 1). This review found many studies focused on relatively small local regions (< 10,000 km^2), and small temporal scales (< 10 years) (Fig. 4). Modes of climatic variability (e.g., ENSO, PDO), which are major drivers of regional ecology, influence statistical uncertainty in climate change signals at regional scales (Bindoff *et al*., 2014). For example, the Gulf of Alaska and Bering Sea fluctuated from one of the warmest years in the past century (2005) to one of the coldest (2008) in the space of three years, driven by the modes of ENSO and PDO and other factors, with associated changes in plankton, fish and seabird communities (McKinnell & Dagg, 2010). This is supported by the findings in this review, with > 25% of studies discussing or including regional climatic variability in their findings or models. Local-scale variability in temperature and primary production can lead to inaccurate interpretations of important performance indicators (e.g., growth and size structure) compared across sites. Similarly, biological responses to environmental change are often idiosyncratic and can occur from local to regional to global scales, depending on species dispersal ability, physiological tolerances, habitat and food preferences, and generation time (O'Connor *et al*., 2012). Research that ignores these biological and environmental differences risks mismatching their study design to the drivers and response mechanisms involved, resulting in high uncertainty and unreliability in their findings. However, such misinterpretations and mismatch of environmental drivers versus biological response can be avoided through appropriate consideration of interannual variability in oceanographic conditions (e.g., oceanographic data anomalies), regional data from ocean observation systems (e.g., upwelling, currents), consideration of regional climatic variability (e.g., ENSO) and knowledge of local-scale conditions (e.g., temperature) (Fig. 1).

Climate change is already having dramatic impacts on oceanic environments, particularly in polar regions which are losing ice (Meredith *et al*., 2019), altering marine primary production (Meier *et al*., 2014), with possible consequences for baleen whales (Tulloch *et al*., 2019). Only nine studies explicitly tested responses of baleen whales to changes in sea-ice, with four times more studies focused on Arctic ecosystems than Antarctic, despite the disproportionate and increasing importance of the Southern Ocean in global ocean heat increase (accounting for 35–43% of the global ocean heat gain in the upper 2,000 m during 1970–2017 (Meredith *et al*., 2019)). No studies explicitly included ocean acidification, sea-level rise, rainfall and runoff, storm frequency, wind speed, wave frequency and other extreme events in their models, despite evidence that these factors are increasing and/or worsening due to climate change and could have potential direct or indirect implications for baleen whales (Learmonth *et al*., 2006; Kawaguchi *et al*., 2013). Although krill may not consume all types of phytoplankton (Haberman *et al*., 2003), Chl_a was frequently used as a proxy for prey in studies. Studies which explicitly link changing oceanic environments to krill and, subsequently, baleen whales in Antarctic waters were extremely rare (e.g., Tulloch *et al*., 2019). An increasing body of work focuses on the direct effects of climate change on krill (McBride *et al*., 2021; Atkinson *et al*., 2022; Kawaguchi *et al*., 2024). This research should be linked to corresponding models of whale-climate change responses to better explore potential indirect impacts of changing prey on baleen whales (e.g., Tulloch *et al*., 2019). Less than half of the studies published on baleen whale responses to climate change included more than one extrinsic environmental factor in their analysis, and most of these used correlative statistical methods.

Local management initiatives to combat climate change typically rely on strategies that increase species or ecosystem resilience to future change by reducing non-climate stressors, such as fishing (Marshall & Schuttenberg, 2006; Stein *et al*., 2013; Gulland *et al*., 2022). Historically, the biggest threat to whales was commercial whaling. Although this practice no longer continues in most regions globally (except for Bryde's, fin, sei and minke whale populations in the North Pacific, targeted by Japanese whaling operations, and fin and minke whales in Norwegian and Icelandic waters), fishing of baleen whale prey is a continuing and potentially growing industry (Nicol *et al*., 2012). Large whales are also affected by a variety of anthropogenic impacts in addition to climate change, including entanglement in fishing gear, vessel strike, exposure to noise (e.g., from seismic exploration), toxins, pollutants and pathogens (Cassoff *et al*., 2011; Pompa *et al*., 2011; Davidson *et al*., 2012; Myers *et al*., 2019). Approaches that include physiological factors could be particularly useful for delineating chronic cumulative impacts, assessing sublethal impacts and establishing mechanistic cause-and-effect linkages (Cooke *et al*., 2013; Hunt *et al*., 2015). More rapid and dynamic implementation of marine mammal management measures is required to address unexpected climate change-induced impacts in a timely fashion (Tittensor *et al*., 2019; Crespo *et al*., 2020). Other management options include climate-ready spatial protection that adapts to moving distributions of krill and their whale predators (Hazen *et al*., 2018), or dynamic spatial zoning as used to manage southern ocean bluefin tuna *(Thunnus maccoyii)* (Hobday *et al*., 2009; Hobday *et al*., 2010). Dynamic models of species' potential range shifts that incorporate population and dispersal processes as well as ecological processes are needed to assess climatic change impacts upon species' relative extinction risks, and to develop conservation management strategies which can adapt to climate change (Hannah *et al*., 2002; Anderson *et al*., 2009; Huntley *et al*., 2010)

The development of fully process-based models may be hindered for many baleen whale species by data deficiencies and associated uncertainty in parameters needed to calibrate these models. Ecosystem models that can explicitly account for interactions and biological processes, such as Models of Intermediate Complexity for Ecosystem Assessments, can help fill gaps in knowledge and can produce robust predictions about how species will react to climate change (e.g., Tulloch *et al*., 2019). Individual-based models (IBM) that incorporate dynamic energy budget theory (Kooijman, 2010) and couple to oceanographic processes have also been proposed, which can account for the key life history and reproductive traits of species that are challenging to model (Goedegebuure *et al*., 2017). Some IBMs have been developed for baleen whales already given present-day SST conditions (e.g., Dodson *et al*., 2020), that could be expanded using outputs from predictive ESM. Alternatively, integrated models that combine climatic suitability, habitat availability and suitability, population dynamics and dispersal may also be a solution in the near-term to address this challenge (Huntley *et al*., 2010). Such models are still in their infancy (Keith *et al*., 2008; Anderson *et al*., 2009).

Process-based models that can dynamically and robustly provide information on species' responses and the causal mechanisms underlying these responses should be considered best practice for inferring climate impacts on whales. These can be more time-consuming and challenging to develop, as well as often requiring physiological information that may be data-deficient for many populations. In the long-term, however, decisions that are made from process-based methodologies that include environmental and physiological information will be more robust and reliable, hopefully resulting in better outcomes for vulnerable whale populations impacted by a changing climate.

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Supplementary Material

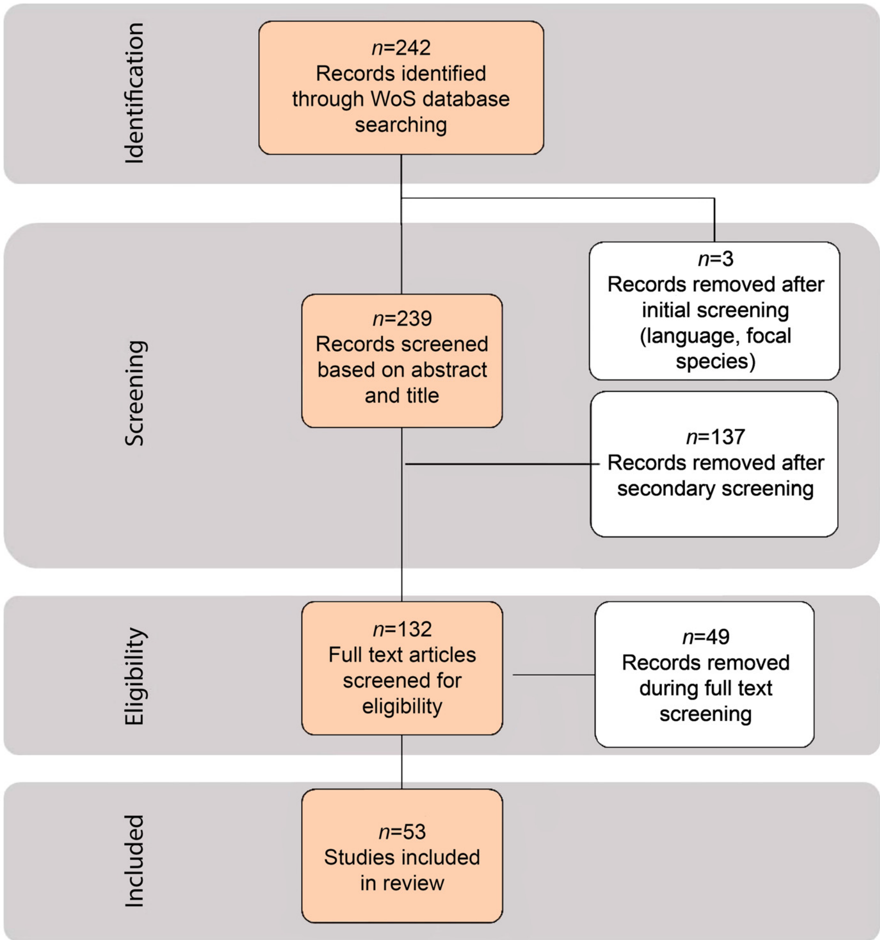

Figure S1. Overview of the systematic review selection process adapted from PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) for the refined literature review (only baleen whales) (Moher *et al*., 2015). The number of papers obtained after each step of the selection process is shown (n = x).

(a) Climate variable	**Inferred**	**Tested**
Chlorophyll (Chl-a)	3	9
Circulation	2	6
Mixed layer depth and stratification	0	4
Ocean acidification	0	0
Salinity	1	4
Sea-ice thickness, extent	9	9
Sea-surface temperature	11	28
(b) Response mechanism	**Inferred**	**Tested**
Adaptive potential/plasticity	2	5
Breeding success/birth rate	1	4
Competition/species interactions	1	3
Diet/foraging dynamics	3	3
Evolution	1	1
Migratory phenology/timing	7	8
Range change	9	17
Survival/mortality	5	2
(c) Study design	**Inferred**	**Tested**
Expert opinion	4	0
Statistical	19	27
Mechanistic	0	2
Simulation	0	1

Figure S2. Counts of the number of instances where: (A) each climate variable was included in analyses, split by whether the authors inferred their conclusion or explicitly tested it; (B) types of climate drivers evaluated; (B) whether study authors suggested different mechanisms to a baleen whale's response to climate change, split by whether the authors inferred their conclusion or explicitly tested it; and (C) study methodological categories, split again by inferred vs. tested. Darker shades highlight more studies.

Table S1

Typology of models used to guide management decisions, identifying constraints and suitability for future-focused climate management.

Modelling approach	Detail	Suitability for future-focused climate management	Constraints	Types of models/methods
Opinion or rule	Based on expert opinion, "rules of thumb", with limited data – qualitative assessment only	Low	High uncertainty; unclear assumptions	Expert elicitation, conceptual models, speculation (Possingham, 1996)
Statistical extrapolation/ correlation	Patterns between variables based on statistical relationships (extrapolative, correlative)	Low	Inappropriate for projection to novel conditions	Regression: LM, GLM, GAM, MARS; machine learning, CART, boosting (BRT, RF), Correlative SDMs (ecological niche models, habitat niche models e.g., Aquamaps), MaxEnt, BIOMOD, bioclimatic envelopes: BIOCLIM (Busby, 1991; Elith and Leathwick, 2009; Guisan *et al.*, 2013)
Process-based (mechanistic)	Based on direct measurements of species' ecophysiological responses to environmental conditions	Excellent	Greater data requirements, more difficult to develop models	Matrix population models (Caswell, 2000; Corkeron *et al.*, 2018); metapopulation models (e.g. Sale *et al.*, 2006); mechanistic niche models (Kearney and Porter, 2009)
Complex simulation models/ecosystem models	Can be process-based, or mixture of rule-based, statistical and process-based components. Mathematical formulations drive simulation rules	Good	Greater data requirements, more difficult to develop models; parameter space can be large, complexity can hinder uptake	Individual-based models (Grimm and Railsback, 2005; Dodson *et al.*, 2020); dynamic bioclimate envelope models (Cheung *et al.*, 2012); dynamic population/ecosystem models (Tulloch *et al.*, 2019b), dynamic spatial simulation models (Overholtz and Link, 2009), end-to-end models (e.g., Atlantis; Link *et al.*, 2010)

Table S2

Five biological mechanisms that determine responses to climate change, examples of model parameters and methods/data requirements (adapted from Urban *et al.*, 2016).

Biological mechanism	Model parameters	Methods and data requirements
1. Physiology	Thermal tolerances; environment-dependent metabolic rate	Experimental data identifying physiological responses to environmental conditions (e.g., from biopsies); observed correlations between physiological responses and environmental conditions in time or space; trait-based proxies (e.g., body mass for metabolism)
2. Demography, life history and phenology	Birth and mortality rates, including breeding success, age of maturity, growth rates, timing, survival at different life stages	Long-term mark recapture studies, historical whaling data, long-term demographic data; studies of birth and death rates in nature; population growth rates from observed abundance data
3. Evolutionary potential and selection/population differentiation	Genetic trait variance/heritability, phenotypic variation including plasticity, fitness differences among populations and environments	Quantitative genetic variation in traits estimated from individuals from common conditions; phenotypic variation within and between populations; correlational estimation of selection
4. Species interactions	Spatio-temporal variation in species interactions, food web links, trophic position, diet or resource competition	Evaluation of species interactions in nature; isotope analysis to reveal trophic levels and food web links, statistical co-occurrence; ecosystem models fitted to population dynamics of predators and prey
Dispersal, range dynamics	Dispersal behaviours, movement, density-and-condition-dependent range, migration patterns	Historical whaling data and historical reconstruction of movement patterns, satellite telemetry and tagging, remote sensing data, mark-recapture, citizen science

Table S3

References for Figure 5 – Northern Hemisphere.

	Change in habitat characteristics of availability						Change to food supply or distribution				Other
Species	Range shift/ contraction	Range shift/ expansion	Habitat change (sea-ice)	Altered breeding/ migratory phenology	Altered predator interaction/ exposure	Altered breeding success/calving rates	Altered prey abundance/ availability	Prey selection/ shifting	Competition for prey	Altered prey accessibility	Direct mortality/ survival
Northern Hemisphere											
Bowhead whale	Moore and Laidre, 2006; Chambault *et al.*, 2022	–	Moore and Laidre, 2006; Chambault *et al.*, 2018; Chambault *et al.*, 2022; Heide-Jørgensen and Laidre, 2004	Tsujii *et al.*, 2021	Ferguson *et al.*, 2010	–	Pomerleau *et al.*, 2017	–	–	–	–
Blue whale	–	Storrie *et al.*, 2018	–	Szesciorka *et al.*, 2020; Ingman *et al.*, 2021	–	–	Szesciorka *et al.*, 2020	–	–	–	–
Common minke whale	Víkingsson *et al.*, 2015; Storrie *et al.*, 2018	Friday *et al.*, 2012	Storrie *et al.*, 2018	–	–	–	Víkingsson *et al.*, 2015	Víkingsson *et al.*, 2015	Víkingsson *et al.*, 2015	Storrie *et al.*, 2018	–
Fin whale	–	Friday *et al.*, 2012; Ramp *et al.*, 2015; Víkingsson *et al.*, 2015; Storrie *et al.*, 2018	–	Ramp *et al.*, 2015, Pendleton *et al.*, 2022b	–	–	Víkingsson *et al.*, 2015	Víkingsson *et al.*, 2015	Víkingsson *et al.*, 2015	–	–
Gray whale	–	Shelden *et al.*, 2004	Shelden *et al.*, 2004; Brüniche-Olsen *et al.*, 2018	Brüniche-Olsen *et al.*, 2018; Ingman *et al.*, 2021	–	Shelden *et al.*, 2004; Salvadeo *et al.*, 2015	–	–	–	Brüniche-Olsen *et al.*, 2018	Warlick *et al.*, 2022
Humpback whale	–	Storrie *et al.*, 2018	–	Ramp *et al.*, 2015; Becker *et al.*, 2019; Cartwright *et al.*, 2019; Ingman *et al.*, 2021; Pelayo-González *et al.*, 2022; Pendleton *et al.*, 2022b	–	Cartwright *et al.*, 2019	Víkingsson *et al.*, 2015	Fleming *et al.*, 2016; Víkingsson *et al.*, 2015	Víkingsson *et al.*, 2015	Becker *et al.*, 2019	Warlick *et al.*, 2022
North Atlantic right whale	Ross *et al.*, 2021	Ganley *et al.*, 2022	Ross *et al.*, 2021	Pendleton *et al.*, 2022a; Ganley *et al.*, 2022; Charif *et al.*, 2020	–	Meyer-Gutbrod *et al.*, 2015	Meyer-Gutbrod *et al.*, 2015; Ross *et al.*, 2021; Ganley *et al.*, 2022	–	–	–	–
North Pacific right whale*	–	Zerbini *et al.*, 2015	–		–	–		–	–	–	–

Table S3

References for Figure 5 – Southern Hemisphere.

	Change in habitat characteristics of availability					Change to food supply or distribution				Other
Species	Range shift/ contraction	Range shift/ expansion	Habitat change (sea-ice)	Altered breeding/ migratory phenology	Altered predator interaction/ exposure	Altered breeding success/calving rates	Altered prey abundance/ availability	Prey selection/ shifting	Competition for prey	Altered prey accessibility	Direct mortality/ survival
Southern Hemisphere											
Antarctic minke whale*	Ainley *et al.*, 2005	–	–	–	–	–	Tulloch *et al.*, 2019a	–	Ainley *et al.*, 2005; Tulloch *et al.*, 2019a	–	–
Blue whale*	–	Peters *et al.*, 2022	–	–	–	–	Tulloch *et al.*, 2019a	–	Tulloch *et al.*, 2019a	–	–
Fin whale*	–	Santora *et al.*, 2014	–	–	–	–	Tulloch *et al.*, 2019a; Santora *et al.*, 2014	–	Tulloch *et al.*, 2019a	–	–
Humpback whale	–	Derville *et al.*, 2019	–	Avila *et al.*, 2020; Horton *et al.*, 2020	–	–	Tulloch *et al.*, 2019a	–	Tulloch *et al.*, 2019a	–	–
Southern right whale	–	Torres *et al.*, 2013	Torres *et al.*, 2013	–	–	Agrelo *et al.*, 2021	Tulloch *et al.*, 2019a	–	Tulloch *et al.*, 2019a	–	Agrelo *et al.*, 2021