



# Impacts of climate change on cetacean distribution, habitat and migration

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## ABSTRACT

Climatic changes have had significant impacts on marine ecosystems, including apex predators such as cetaceans. A more complete understanding of the potential impacts of climate change on cetaceans is necessary to ensure their conservation. Here we present a review of the literature on the impacts of climate change on cetacean distribution, habitat and migrations and highlight research gaps. Our results indicate that due to rising sea surface temperatures (SSTs) and/or reducing sea ice extent, a variety of impacts on the distribution, habitat and migration of cetaceans have been observed to date and several more are predicted to occur over the next century. Many species have demonstrated a poleward shift, following their preferred SSTs to higher latitudes, and some have altered the timing of their migrations, while others appear not to be affected. These changes may benefit certain species, while others will be placed under extreme pressure and may face increased risk of extinction. Broader implications may include increased inter-specific competition, genetic alterations, ecosystem-level changes and conservation challenges. Existing research on the topic is both extremely limited and unevenly distributed (geographically and phylogenetically). Further research is necessary to determine which species and populations are most vulnerable and require the earliest conservation action.

## 1. Introduction

Anthropogenic activity has caused the Earth's climate to change at such a rate that the effects may be irreversible [21,42,99]. These climatic changes have had severe impacts on marine ecosystems, including fluctuations in ocean temperature and chemical composition, primary productivity and the distribution and abundance of species [4,17,42,76]. The combination of changes in oceanic conditions and prey distribution and abundance are likely to impact marine predators at higher trophic levels, including cetaceans [4,89]. However, the exact effects of climate change on marine megafauna, including cetaceans, remain uncertain [26].

Cetaceans play a key and irreplaceable role in marine ecosystems and have been referred to as 'ecosystem engineers', crucial for oceanic nutrient cycling [4,81,28]. For example, the faecal plumes they release near the surface contain deep ocean nutrients which would otherwise be unavailable to surface-dwelling species [54,82]. Their faeces are particularly high in iron and nitrogen, which are both required for phytoplankton blooms, the primary prey of Antarctic krill (*Euphausia superba*) [72,81]. Cetaceans are also known to be vital in controlling prey populations [20,97] and creating feeding opportunities for marine birds [27]. These large marine mammals, which are still recovering from the severe impacts of the whaling era and are already under extreme pressure from

various other anthropogenic stresses such as plastic [5,24,74], chemical [45,62] and noise pollution [47,71,108], must also tolerate both small and large-scale climatic changes [83]. Due to these stressors, multiple cetacean populations may eventually collapse, which could result in permanent, long term consequences for marine ecosystem functioning and services [4]. For these reasons, cetacean conservation should be a priority.

Cetaceans are difficult to study due to their high mobility, the amount of time they spend under water, and the legal and political constraints of researching protected species [11]. Nonetheless, some research on the influence of climate change has been conducted and a variety of impacts on cetaceans have been observed to date. Documented population level impacts include changes in distribution [53,100], shifts in the timing and duration of migrations [78,84], habitat loss [29,37], and reduced conception rate and reproductive success [19,26,66,90]. Two examples of observed impacts at an individual level are increased mortality due to algal blooms [10,36,57] and enhanced mercury bioaccumulation [12,58].

To increase conservation success, a more complete understanding of the potential impacts of climate change on cetaceans is necessary, and insights into the potential climate-induced changes in their distribution and movements are especially important for two reasons. Firstly, such insights will help enable impacts of threats (e.g. shipping routes and pol-

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lution) associated with distributional changes to be predicted. Secondly, they will facilitate improved conservation through the implementation of new Marine Protected Areas (MPAs) and adaptation of both local and global policies. Importantly, a thorough review of all existing literature on the topic has not been conducted since 2009 [55,59,94]. In the past decade, there has been a significant amount of research published, which warrants an updated literature review. Therefore, the research objectives of this qualitative systematic literature review are to summarise the current literature on the impact of climate change on cetacean distribution, habitat and migration and highlight the research gaps. Based on the review we will provide suggestions for future research as well as a basis from which well-informed conservation strategies and policies can be devised and implemented.

## 2. Methodology

### 2.1. Methodological justification

This literature-based research was carried out according to the Systematic Literature Review (SLR) method described by Siddaway et al. [93]. The Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) checklist and flow diagram were also used [68]. This established systematic literature review method was used to summarise existing knowledge regarding the observed and predicted impacts of climate change on cetacean distribution, habitat and migration. By synthesising existing knowledge on the topic, this review will highlight areas which require the most urgent future research as well as act as a starting point for developing policies and population management plans to protect species that may already be at risk.

### 2.2. Search terms

A search string consisting of several search terms has been chosen to cover the variation in terminology used in publications on this topic. Subject keywords ‘cetacean’, ‘whale’, ‘dolphin’ or ‘porpoise’ were combined with exposure keywords “climate change” or “global warming”. The associated search string was run through the Web of Science and PubMed with a cut-off date of July 22<sup>nd</sup>, 2020. Web of Science and PubMed are two high-quality search engines and were employed to increase chances of covering all relevant results [31,93,109].

### 2.3. Screening and eligibility

All non-peer-reviewed articles as well as those not written in English and any duplicates were excluded immediately (Fig. 1). Subsequently, papers were excluded if not deemed relevant following a screening of the titles and abstracts. At this stage (screening), papers were excluded if they met one or more of the following criteria:

- I not focused on impacts on cetacean distribution, habitat or migration;
- II not climate change related;
- III review with no primary data;
- IV had a study period of <5 years or <5 years of relevant data;
- V focus on developing/testing a new methodology/concept;
- VI focus on El Niño-Southern Oscillation (ENSO), Northern Atlantic Oscillation (NAO) or Pacific decadal oscillation (PDO).

If the relevance of a paper remained uncertain based on its abstract, it was included at this stage with the aim of maintaining the high sensitivity recommended by Siddaway et al. [93]. If papers were excluded based on lack of relevance, a brief explanation was also recorded. Papers that were initially included were assigned keywords to facilitate further research and write-up about specific topics. Examples of common key words were range changes; migration changes; sea ice changes.

In the next step, the remaining papers were read in full and were excluded if they met one or more of the same exclusion criteria described above. A table detailing borderline cases, the inclusion/exclusion decision and reasoning can be found in the supplementary information (Table S1). For the included papers, the species, location, method and key findings were recorded. Finally, the bibliographies of included papers, along with several review papers excluded during the screening process, were scanned in search of other potential sources. Any papers found through this method underwent the same selection criteria as the rest of the papers. These additional papers were only included when their content seemed essential for the narrative of the literature review. This method of locating additional sources proved crucial in understanding the impact of climate change on cetaceans, given the low level of existing research on the topic.

### 2.4. Establishing geographical categories

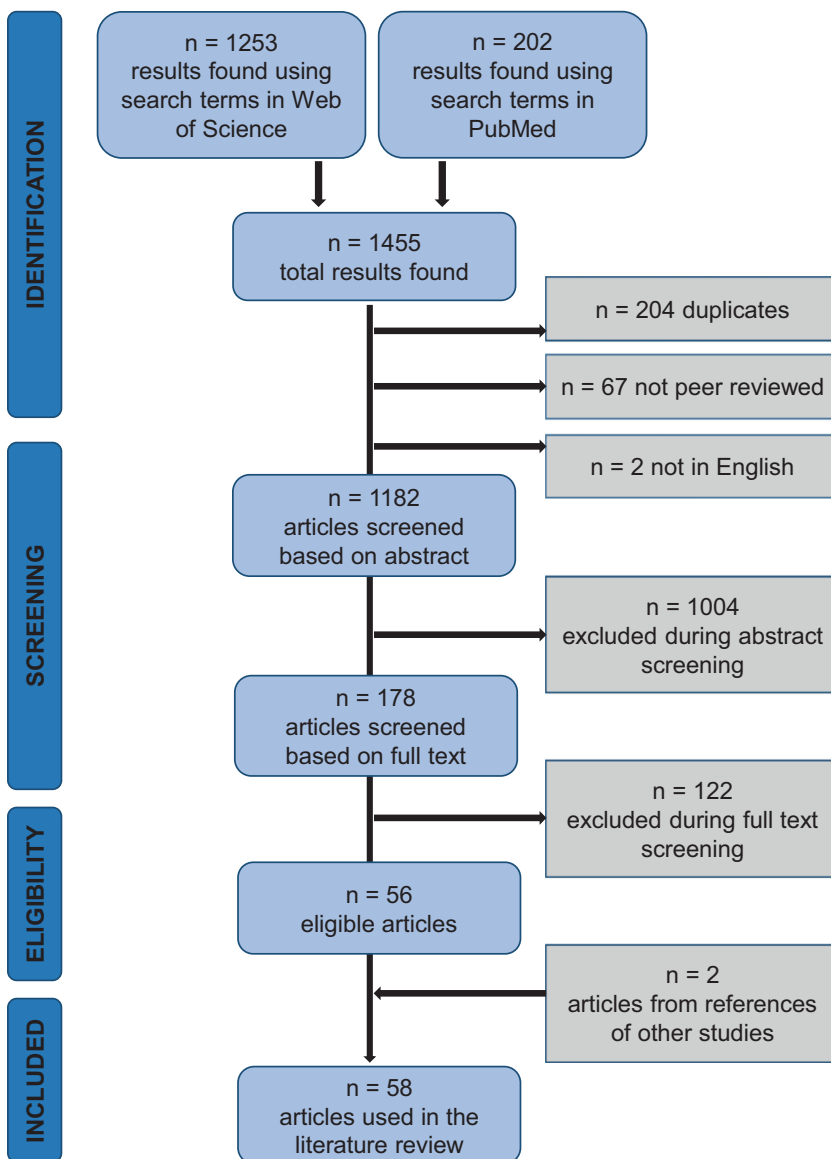
All papers meeting the inclusion criteria were split into two sections: those that described observed impacts and those that predicted future impacts. If an article included both observed and predicted impacts, it was included in both sections. Next, papers were sorted based on species, and papers focussing on multiple species were included in the sub-sections of all relevant species. Finally, species were categorised based on either their geographic range or the location of the studies they were described in. For example, the narwhal, beluga and bowhead whale were categorised as ‘Arctic resident species’ because they remain there year-round [37]. On the other hand, fin and killer whales were included in both the Subarctic category, as well as the ‘Other regions’ category, since included studies described impacts on these species in both areas.

## 3. Results

### 3.1. Literature searches and screening

Searches in Web of Science and PubMed returned a total of 1,253 results, 273 of which were immediately excluded as they were either duplicates (n=204), not peer reviewed articles (n=67) or not written in English (n=2; Fig. 1). Screening based on title and abstract left 178 articles that were considered as potentially relevant. Following screening based on full text, a further 122 articles were excluded. The main reason for exclusion at this stage was a lack of focus on cetacean distribution, habitat or migration (n=49; Table S2). An additional two articles found in the references of other articles were added which resulted in 58 articles being included in the final review.

Of these 58 articles, 11 modelled future predictions for available habitat over the next century, 46 reported results from studies and distance sampling surveys ranging from 1900-2018 and one investigated both future predictions and past observations. The locations of the studies were unevenly distributed with many (n=21) situated in the vicinity of the continent of North America. All but four of the studies on observed impacts took place in the northern hemisphere, between approximately 0 and 85°N (Fig. 2A). Five out of the 12 articles predicting future impacts modelled scenarios for the Southern Ocean and Australasia. Not all families in the cetacea order were equally represented in the literature (Fig. 2B). In total, 29 species were discussed (see Table S3). Balaenopteridae was by far the most researched family, with members of this family being mentioned in 19 papers (Fig. 2B). No freshwater dolphins (Platanistidae, Iniidae and Pontoporidae) or pygmy/dwarf species [Cetotheriidae, Kogiidae and pygmy killer whales (*Feresa attenuata*)] were discussed in any of the included articles (Fig. 2B). Firstly, the impacts observed to date will be described (Fig. 3, Table S4, S5), followed by those predicted to occur over the next 100 years (Fig. 4, Table S6, S7).



**Fig. 1.** Overview of the systematic review selection process adapted from Moher et al.'s [68] PRISMA (Preferred Reporting Items for Systematic reviews and Meta-Analyses) statement and Siddaway et al.'s [93] best practice guidelines. The number of papers obtained after each step of the selection process is shown ( $n = x$ ).

### 3.2.1. Arctic

Of the 58 studies included, 12 focused on the impacts of climate change on one or more of the three resident Arctic species, the bowhead whale (*Balaena mysticetus*; Fig. 3, Table S4), the beluga (*Delphinapterus leucas*; Fig. 3, Table S5), and the narwhal (*Monodon monoceros*; Fig. 3, Table S5), which are believed to be among the most vulnerable to climatic changes [33,37,107]. Surprisingly, despite rising average SSTs, several of the crucial (Canadian) wintering grounds of all three species showed significant *declining* trends in the fraction of open water during winter between 1979-2001, and only a minority showed a slight increasing trend [37]. Two important narwhal wintering grounds in Baffin Bay (Greenland) displayed high inter-annual variability in ice cover alongside an overall decreasing trend [51]. Contrastingly, all large bowhead wintering grounds and 12 of the 16 smaller ones displayed a weak positive trend in the fraction of open water between 1979 and 2002, with extreme interannual variability [70].

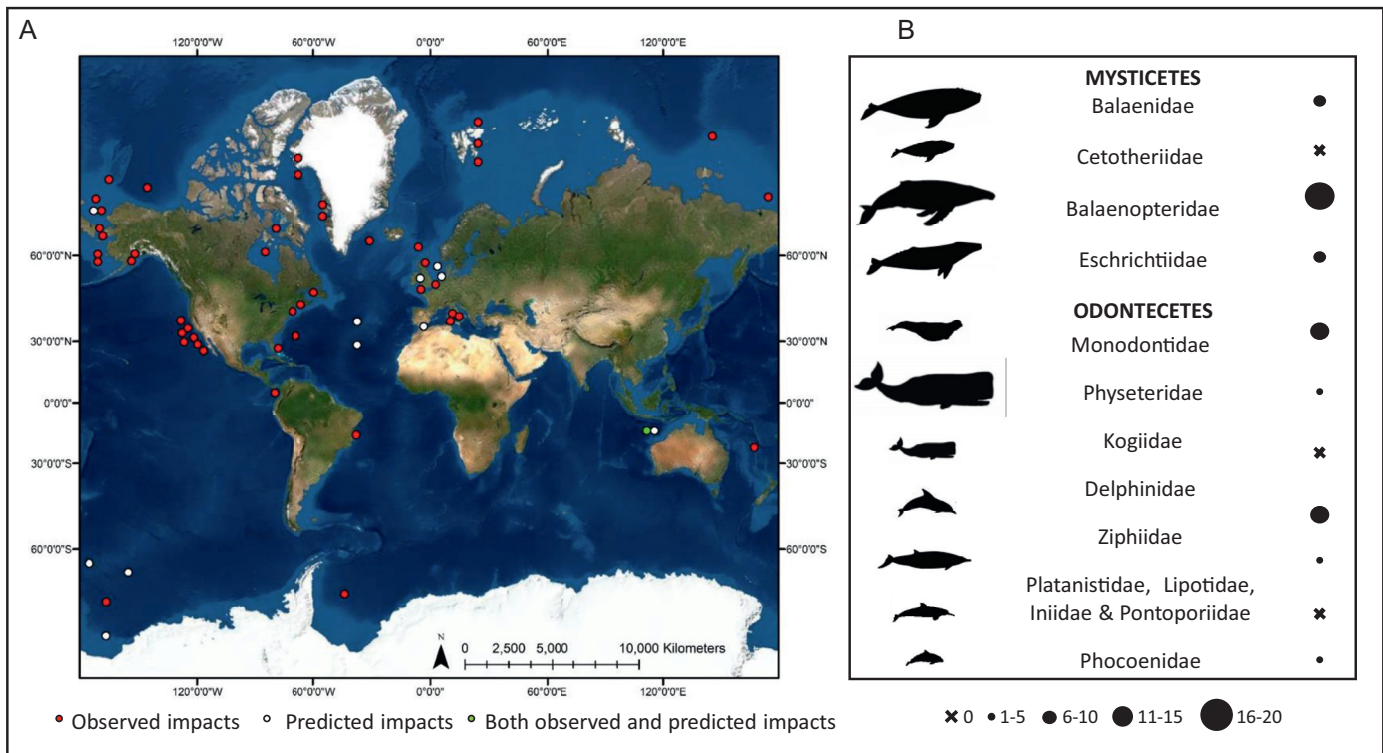
Shift in beluga sightings were observed in several studies (Fig. 3, Table S5). For example, an increase in sightings was found in the Svalbard Archipelago and northward shift in sightings in Disko Bay (Greenland) which coincided with warming SSTs [38,100]. They expanded their range to western Greenland when the sea ice contracted to the

east in 2006, but this was reversed when the sea ice increased again in 2007-2008 [38]. A >300% increase in sightings was observed in the offshore Beaufort Sea from the 1980s ( $n=305$ ) to the 2000s ( $n=1061$ ), which cannot be accounted for by population growth alone [34]. Beluga also spent significantly less time near tidal glacier fronts between 2013 and 2016 compared to 1995-2001 [33,107].

Beluga migration also showed changes. For example, migration from the Beaufort Sea to the Chukchi Sea was between 14 and 33 days later in 2007-2012 compared to 1993-2002, and the last day individuals left the Beaufort Sea was delayed by 4.1 days each year between 2008 and 2013 [35]. Similarly, the beluga population resident to the Gulf of Alaska entered the Cook Inlet earlier and extended their stay there in warmer years [30]. In contrast, O'Corry-Crowe et al. [73] found no significant changes in the date that beluga returned to Kasegaluk Lagoon (Alaska) between 1979 and 2013.

### 3.2.2. Subarctic

A significant increase in the sightings of three subarctic baleen whale species - humpback whales (*Megaptera novaeangliae*), fin whales (*Balaenoptera physalus*) and common minke whales (*Balaenoptera acutorostrata*) - in the Arctic over the past few decades has been observed



**Fig. 2.** A) Locations of studies on cetaceans included in the literature review; B) Number of studies included in the literature review per family. Sources: Esri, GEBCO, NOAA, National Geographic, DeLorme, HERE, Geonames.org.3.2 Observed Impacts

[14,100]. All three species displayed a northward shift between 2002 and 2014, with their annual maximum latitude increasing by 2°, 1° and 1°, respectively [100]. The blue whale (*Balaenoptera musculus*) has shown a 4° increase in annual maximum latitude [100].

Humpback and fin whale migrations to their summer feeding ground in the Gulf of St. Lawrence, Canada, took place earlier in the year, with each species' mean first arrival date shifting 1+ day(s) earlier each year between 1987 and 2010 [78]. Fin whales extended their stay in the gulf by an average of 16 days over the duration of the study period [78]. Blue whales which feed off the west coast of California and those off the south west coast of Columbia were arriving at their feeding grounds >1 month earlier in 2018 and 2017 compared to 1988 and 2008, respectively [9,102]. Their departure dates have remained relatively stable over the same period resulting in significantly increased occupancy and feeding periods.

Grey whale (*Eschrichtius robustus*; another seasonal Arctic resident) displayed a 1-week delay in the southbound migration, which passed Yaquina Head (Oregon) around the 8<sup>th</sup> of January prior to 1980 compared to the 15<sup>th</sup> of January after 1980 [84]. In addition, the increase in grey whale calf sightings on the southbound migration along the west coast of the US from 1952-2002 suggests a shift in calving grounds [91]. Prior to 1976, no new-born calves were observed on this period of the migration, but from 1976 onwards there was an increase in calf sightings farther north.

At a local scale impacts were also observed. North Pacific Right Whales (*Eubalaena japonica*) tagged in cold years (2008-2009) remained in the middle of the Bering Shelf, travelled more slowly and covered a smaller area than those tagged in the warm year (2004). A closely related species, the North Atlantic Right Whale (*Eubalaena glacialis*), has exhibited a sudden shift from early to late occupancy in the Bay of Fundy (Canada) in 2002 [25], and calls have been increasingly detected outside the feeding season in Massachusetts Bay between 2007 and 2013 [111].

Two species of subarctic toothed whale are also becoming more prevalent in Arctic waters [40,100]. Sperm whales (*Physeter macrocephalus*) have demonstrated a northward shift in average maximum latitude from 76°N in 2002 to 79°N in 2014 [100]. The number of killer whales (*Orcinus orca*) sightings per decade in the Canadian Arctic has increased rapidly from 5 in 1900, to 30 in 1990 and 140 in 2000 and both the number of days and hours of detected calls have risen from 2009-2015 [41,112]. Further evidence of increased killer whale presence is the increase in percentage of bowhead whales in the same region with scarring from killer whale rake marks, from ~2% (1986) to ~9% (2007-2010) to ~15% (2011-2012) [79]. However, Ainley et al. [2] reported a decrease in sightings and proportion of days seen in the Ross Sea.

### 3.2.3. Other regions

Both Bryde's whales and fin whales appear to have displayed distributional shifts as a result of rising SSTs. Bryde's whale (*Balaenoptera edeni*) calls were not recorded in the Southern Californian Bight between 2000 and 2001, but were recorded every year between 2003 and 2010 [49]. Fin whale sightings in the Tyrrhenian Sea (Italy) increased by 300% from 0.08 sightings per hour of effort (ER) between 1990 and 1992 to 0.36 ER between 2007 and 2009 [7]. In contrast, common bottlenose dolphin (*Tursiops truncatus*), Cuvier's beaked whale (*Ziphius cavirostris*) and striped dolphin (*Stenella coeruleoalba*) sightings in the Tyrrhenian Sea did not differ between 1990-1992 and 2007-2009, despite a marked rise in SST [7].

Long-term stranding data sets have been used a proxy for presence in order to explore the impact of climate change on the distribution of marine mammals. A study into seasonal and interannual patterns of marine mammal strandings in the subtropical western south Atlantic, recorded temperate/polar species strandings since the early 1980s while tropical/subtropical species strandings only occurred after 1993 [77]. These findings suggest a poleward expansion of warm-water species. Four cold-temperate water species, northern bottlenose

		Observed Impacts						
		maximum latitude	habitat availability	migration dates	time spent in high latitude	visual/acoustic detections	strandings	other
Region	Species							
Arctic	Bowhead whale		↓					
	Narwhal		↓					
	Beluga		↓	↓		↑	↓	
Subarctic	Humpback whale	↑		↑	↑	↑		
	Fin whale	↑		↑	↑	↑		
	Common minke whale	↑				↑		
	Blue whale	↑		↑	↑			
	Sperm whale	↑						
	Killer whale					↑	↓	↓
	Grey whale			↓				□
	North Pacific right whale							□
	North Atlantic right whale					↑		
	Other	Bryde's whale					↑	
Humpback whale						↑		
Fin whale						↑		
Blue whale						↓		
Antarctic minke whale						□		
Killer whale							↓	
Northern bottlenose whale							↓	
Long-finned pilot whale							↓	
Short-finned pilot whale								□
Sowerby's beaked whale							↓	
White beaked dolphin						↓		

Fig. 3. Trends in observed impacts of climate change on cetacean distribution, habitat and migration. Green with upward arrow signifies an increase (earlier regarding migration), red with downward arrow signifies decrease (later regarding migration), orange signifies no change and light blue signifies other changes with no clear trend.

whales (*Hyperoodon ampullatus*), long-finned pilot whales (*Globicephala melas*), Sowerby's beaked whales (*Mesoplodon bidens*) and white-beaked dolphins (*Lagenorhynchus albirostris*), all stranded in north-west Scotland significantly less frequently between 1992 and 2003 than between 1948 and 1992 [60]. However, killer whales, which are considered to withstand a wide range of SSTs, also stranded less frequently in 1992-2003, highlighting that other factors might have influenced this change in standing patterns [60]. In contrast, harbour porpoise (*Phocoena phocoena*) and short-beaked common dolphin (*Delphinus delphis*) strandings in the area showed an opposite trend [44,56,60]. This highlights a shift in habitat in the region, favouring warm-water species over cold-water species.

	Harbour porpoise								↑
	Short beaked common dolphin	↑							↑
	Common bottlenose dolphin						□		
	Cuvier's beaked whale						□		
	Striped dolphin						□		
	Pacific white-sided dolphin	↑	↓				↓		
	Northern right whale dolphin	↑	↓						
	Dall's porpoise	↑	↓						
	Atlantic spotted dolphin								□
	Tropical/subtropical species								↑

Fig. 3. Continued

		Predicted Impacts			
		maximum latitude	habitat availability	occurrence	other
Region	Species				
Arctic	N/A				
Subarctic	Humpback whale	↑	↓		
	Fin whale	↑	↓		
	Common minke whale	↑	↓	↓	
	Blue whale	↑	↓		
	Sperm whale	↑	↓		
	Grey whale	↑	↑		
	North Pacific right whale		↑		
	North Atlantic right whale		↑		
	Other	Antarctic minke whale	↑	↓	
Southern Right Whale		↑	↓		
Harbour porpoise		□			□
Short beaked common dolphin		□	↓	↑	
Cuvier's beaked whale		↑	↓	↓	
Striped dolphin		↑	↑	↑	

Fig. 4. Trends in predicted impacts of climate change on cetacean distribution, habitat and migration. Green with upward arrow signifies an increase, red with downward arrow signifies decrease, orange signifies no change and light blue signifies other changes with no clear trend. Occurrence refers to whichever region the article is discussing.

### 3.3. Predicted impacts

#### 3.3.1. Southern ocean

Two studies have projected adverse impacts of climate change on Antarctic minke whales (*Balaenoptera bonaerensis*), and predicted significant reductions in suitable habitat (Fig. 4, Table S6; [3,106]). However, Tulloch et al. [105] proposed that the predicted southward range shift to 70–80°S will benefit the species, as it will result in an increased access to energy-rich prey. On the contrary, southern right whales (*Eubalaena australis*) may experience a reduction in prey availability around 2100 following a southward range shift to 47–50°S [104,105].

A study on the impacts of a 2°C rise in global air temperature on cetaceans in the Southern Ocean found that humpback whales, fin whales, blue whales (Fig. 4, Table S6) and sperm whales (Fig. 4, Table S7) are predicted to display a southward shift and contraction of foraging habitat due to a similar shift of the Antarctic Circumpolar Current (ACC) [106]. Finally, many humpback breeding grounds in Oceania are predicted to become unsuitably warm by the end of the 21<sup>st</sup> century [26].

#### 3.3.2. Other regions

A study investigating current and future patterns of global marine mammal biodiversity, including cetaceans, found that 54% of marine mammal species are predicted to experience an increase in habitat by 2040–2049 based on the intermediate IPCC-A1B climate change scenario, while 45% are predicted to experience a reduction and 1% are predicted not to be affected [46]. Despite most of these changes being <10% per taxa, North Pacific right whales, North Atlantic right whales and grey whales are predicted to benefit from more substantial increases in suitable habitat (Fig. 4, Table S6; 15%, 27% and 40% increase in habitat, respectively). Projections of grey whale distribution in 2100 by Alter et al. [6] also suggest an increase in suitable habitat around Canada, Greenland and the Barents Sea alongside a northward shift in range and Brüniche-Olsen et al. [15] predict an improvement of currently marginal habitats in the Arctic (Fig. 4; Table S6).

Lambert et al. [53] employed a bio-climatic envelope modelling technique to predict the impacts of three different future climate change scenarios on several cetacean species in the Eastern North Atlantic. The common minke whale is predicted to undergo a northward range contraction due to reduced availability of suitable habitat and summer feeding grounds in UK and Irish waters (Fig. 4, Table S6; [53]). The summer occurrence of white-beaked dolphin in the area was also projected to drop, while Cuvier's beaked whale is likely to experience a northward range contraction with significant reductions in summer occurrence by 2090 [53]. In contrast, striped dolphins were predicted to undergo a northward range expansion and an increase in summer occurrence [53].

Sadykova et al. [85] demonstrated how incorporating different prey species into predictive models can significantly alter the predicted outcomes of climate change. Within this model the impacts of climate change were predicted based on the biology of the harbour porpoise (single-species model), but also on the combined biology of harbour porpoise and important prey species (herring or sandeel; joint-models). The single-species harbour porpoise model and the joint herring-harbour porpoise model predicted no large distribution shifts, however, the joint sandeel-harbour porpoise model predicted a large distribution shift of 164km southwest [85].

Finally, an article by Cañadas and Vázquez [18] created a model to predict the impact of rising SST on short-beaked common dolphins in the Alboran Sea over the next 100 years (Fig. 4; Table S7). The results showed no change in their distribution but suggested a decrease in the amount of suitable habitat followed by a predicted reduction in density from east to west. However, predictions of this species range in the Northeast Atlantic display a significant northwards range expansion within the next few decades [52].

## 4. Discussion

Due to rising SSTs and/or reducing sea ice extent, a variety of impacts on the distribution, habitat and migration of cetaceans have been observed to date and several more are predicted to occur over the next century. A considerable number of studies have focused on the observed impacts, highlighting that most species have demonstrated a poleward shift, following their preferred SSTs to higher latitudes (e.g. [38,53,100]). The contrasting trends in reducing fractions of open water in wintering grounds and decreasing Arctic Sea ice cover have resulted in a reduction in the amount of suitable habitat for the three residential Arctic cetaceans [37,51]. Subarctic species, such as humpback and fin whales, are showing increasing presence in the Arctic, which is likely to continue with projected decreasing sea ice trends [14,100]. In addition, the migration timing of several species have also been delayed or advanced [35,78,84]. In contrast, the distribution of certain populations of particular species, including bottlenose dolphins, striped dolphins and Cuvier's beaked whales, does not appear to be impacted by climatic changes/rising SST [7].

Surprisingly, given the recent advances in climate and ecosystem modelling, very few articles have attempted to predict future impacts of climate change on cetacean distribution and habitat (n=12). In most of the studies that did, cetaceans are forecasted to shift their distribution to higher latitudes [53,104–106]. These shifts will result in a severe reduction in suitable habitat by 2100 for eight out of the 14 species investigated. Northern Atlantic right whales, North Pacific white whales, grey whales and striped dolphins are predicted to experience range expansions. It is understandable that striped dolphins would benefit from increased SSTs due to their preference for warmer water conditions, but the three other species predicted expansions are due to melting sea ice cover [53].

Our results are in line with the latest two previous reviews on this topic, which described similar findings on the 29 species covered in this review ([55] and [59]; Table 1). Many of the potential impacts of climate change on species range outlined by Learmonth et al. [55] and MacLeod [59] are already apparent in the observed impacts reported in this review, despite only ten years having passed. For example, short-beaked common dolphins have expanded their range northward in UK waters [56,60], while narwhal, beluga and bowhead whales have all suffered reductions in the amount of suitable wintering habitats [37,51].

The increase in SST is an important determinant for species' distributions, and Arctic cetaceans are thought to be especially sensitive due to a reduction of their preferred habitats (e.g., [33,37,107]). Indeed, the results of this review, as well as those by Learmonth et al. [55] and MacLeod [59], suggest that Arctic species have already undergone some of the most severe reductions in range and suitable habitat due to rising SSTs. Other species which prefer cooler waters are also suffering (less severe) reductions in suitable habitat, while those that prefer warm water are benefiting from the opposite. For example, the suitable habitat of white-beaked dolphins (temperate-water species) in Scottish waters decreased as the SST rose between 1948 and 2003, which resulted in reduced presence, whereas short-beaked common dolphins (warm-water species) displayed an antagonistic trend in occupancy due to an expansion of suitable range in the same area [60].

On the other hand, the overall distribution of traditionally widespread species that are comfortable in a range of SSTs, such as humpback, fin and sperm whales, has not been greatly impacted and trends of reduced sea ice could allow them prolonged access to high nutrient waters of the polar regions [14,106]. As a result, species such as humpback, fin and blue whales (widespread) along with striped dolphins (warm water), appear significantly less vulnerable to climatic changes than narwhal, beluga, bowhead whales (Arctic) and white-beaked dolphins (temperate-water). Interestingly, these are not the same species that are considered most vulnerable by the IUCN (Table 1). Since the IUCN Red List is the most widely used system for identifying species

**Table 1**

Comparison of impact on species range/distribution reported by Learmonth et al. [55], MacLeod [59] and this study's review along with IUCN status (2020-2021)

Species	IUCN Status	Learmonth et al. [55]	MacLeod et al. [59]	Current review
<b>Mysticetes</b>				
Bowhead whale ( <i>Balaena mysticetus</i> )	LC	contraction	contraction (high risk for Sea of Okhotsk population)	contraction
North Pacific right whale ( <i>Eubalaena japonica</i> )	EN	unknown	northward shift	unknown
North Atlantic right whale ( <i>Eubalaena glacialis</i> )	CR	contraction	contraction	unknown
Southern right whale ( <i>Eubalaena australis</i> )	LC	contraction (uncertain)	southward shift/contraction (high risk for population that breeds in coastal waters of South Africa)	predicted shift southwards
Humpback whale ( <i>Megaptera novaeangliae</i> )	LC	unknown	unchanged	Northward expansion (population in Southern Ocean predicted to shift southward)
Fin whale ( <i>Balaenoptera physalus</i> )	VU	unknown	unchanged	Northward expansion (population in Southern Ocean predicted to shift southward)
Blue whale ( <i>Balaenoptera musculus</i> )	EN	unknown	unchanged	unchanged (population in Southern Ocean predicted to shift southward)
Common minke whale ( <i>Balaenoptera acutorostrata</i> )	LC	unknown	unchanged (southward expansion of dwarf sub-species)	unchanged with predicted contraction
Antarctic minke whale ( <i>Balaenoptera bonaerensis</i> )	NT	unknown	unchanged	predicted contraction and shift southward
Bryde's whale ( <i>Balaenoptera edeni</i> )	LC	unknown	expansion	expansion/shift northwards
Grey whale ( <i>Eschrichtius robustus</i> )	LC	unknown	expansion	Unchanged/predicted expansion
<b>Odontocetes</b>				
Narwhal ( <i>Monodon monoceros</i> )	LC	contraction	contraction (potentially high risk if Arctic Sea disappears)	contraction
Beluga ( <i>Delphinapterus leucas</i> )	LC	contraction	contraction (potentially high risk for some populations)	contraction
<b>Species</b>				
Sperm whale ( <i>Physeter macrocephalus</i> )	VU	unknown	Mostly unchanged with some expansion	unchanged (population in Southern Ocean predicted to shift southward)
Common bottlenose dolphin ( <i>Tursiops truncatus</i> )	LC	expansion	expansion	unchanged/shift northward
Short-beaked common dolphin ( <i>Delphinus delphis</i> )	LC	expansion (uncertain)	expansion	Northward expansion (predicted contraction for population in the Alboran Sea)
White-beaked dolphin ( <i>Lagenorhynchus albirostris</i> )	LC	unknown	northward shift (high risk for population around north-west Europe)	contraction/shift northwards (predicted to exacerbate)
Pacific white-sided dolphin ( <i>Lagenorhynchus obliquidens</i> )	LC	contraction	northward expansion	northward contraction
Striped dolphin ( <i>Stenella coeruleoalba</i> )	LC	expansion (uncertain)	expansion	unchanged with predicted expansion
Atlantic spotted dolphin ( <i>Stenella frontalis</i> )	LC	expansion	expansion	unknown
Killer whale ( <i>Orcinus orca</i> )	DD	unknown	unchanged	shift northwards
Northern right whale dolphin ( <i>Lissodelphis borealis</i> )	LC	unknown	northward expansion	northward contraction
Long-finned pilot whale ( <i>Globicephala melas</i> )	LC	unknown	poleward expansion (high risk for Mediterranean population)	shift northwards
Short-finned pilot whale ( <i>Globicephala macrorhynchus</i> )	LC	expansion	expansion	unknown
Sowerby's beaked whale ( <i>Mesoplodon bidens</i> )	DD	unknown	poleward expansion	shift northwards
Northern bottlenose whale ( <i>Hyperoodon ampullatus</i> )	DD	contraction	contraction	shift northwards
Cuvier's beaked whale ( <i>Ziphius cavirostris</i> )	LC	Unknown	expansion	unchanged
Harbour porpoise ( <i>Phocoena phocoena</i> )	LC	contraction (uncertain)	northward expansion (high risk for North-West European populations)	expansion/shift northwards
Dall's porpoise ( <i>Phocoenoides dalli</i> )	LC	Unknown	expansion	Northward contraction

N.B. LC = Least Concern; NT = Near Threatened; VU = Vulnerable; EN = Endangered; DD = Data Deficient

\* shift = no significant change in total area of the species' range

at risk of extinction, it has been suggested that its criteria should be adapted to take into account sensitivity to current and future climatic changes [4,22,98]. However, it should be noted that this review has only considered the impacts of climate change on species distribution. A full review of all other potential impacts, including pollution and fisheries'

bycatch and competition, would be necessary in order to assess vulnerability more accurately.

Although most of our findings are in line with Learmonth et al. [55] and MacLeod [59], we did find several differences (Table 1). MacLeod [59] stated that the impacts of climate change on the range of Cuvier's beaked whale would be favourable, whereas the current find-

ings suggest that it has not yet been impacted [7]. Similarly, both Learmonth et al. [55] and MacLeod [59] reported that common bottlenose dolphins and striped dolphins had benefitted from increased habitat due to rising SSTs, while we did not find evidence of such changes to date. Nevertheless, striped dolphins were predicted to expand their distribution over the course of the next century [53]. Despite no positive changes having been observed to date, both common bottlenose dolphins and striped dolphins are commonly found in warmer waters and, therefore, may be less sensitive to rising SSTs [53,59]. These differences in findings are most likely due to a focus on distinct populations of each species. Therefore, the impacts of climate change on multiple distinct populations of the same species should be investigated to prevent contradictory understandings of the species' overall vulnerability.

There are several potential explanation(s) for the observed and predicted impacts described above. Cetaceans are endothermic, well-insulated, and, for the most part, relatively large mammals, which makes it unlikely that range changes are due to a direct relationship between a species' thermal limits and the water temperature ([55,95]; MacLeod et al. [59]). Rather, changes in physical barriers, such as the extent of sea ice, may explain certain shifts in distribution and migration patterns (Heide-Jørgensen et al. [37,39]). For example, sea ice extent has historically limited killer whale movement in the Arctic to the warmer months, but this is changing as the ice-free period is extended due to rising SSTs [40,41,64]. Grey whales also appear to be benefiting from the reduced sea-ice cover as individuals have recently been documented in the North and South Atlantic after presumably transiting through Arctic waters from the Pacific Ocean [6].

In addition, the habitat preferences of marine mammals are known to be ecologically related to the distribution of preferred prey species. The distributions of these prey species are, in turn, determined by the complex combination of oceanographic conditions present, such as temperature, salinity, depth, slope, and nutrient concentration [95]. Therefore, further research is required to better understand the predicted movement of prey species, which would subsequently allow for the changes in cetacean distribution and migrations to be modelled more accurately.

At a more localised scale, competition between two or more ecologically similar species can result in niche partitioning, which may impact a species distribution in that area [59]. For instance, following a rise in SST in Scottish waters, short-beaked common dolphins were found in the same areas as white-beaked dolphins [61]. The common dolphin outcompeted its white-beaked counterpart, which caused white-beaked dolphins to stay in waters of less than 13°C, while common dolphins were found in any waters above 14°C [61]. It is most probable that the observed and predicted distributional changes are controlled by a combination of physical barriers, prey movements and inter-specific competition.

Our results indicated four key implications of the observed and predicted changes on cetaceans. Firstly, distributional changes are likely to result in the overlap of species' ranges, which may lead to increased inter-specific competition [14,32,100]. For example, the greater competition for euphausiids and copepods, by subarctic species such as humpback and fin whales, may put additional pressure on the already vulnerable Arctic residents [14,69]. Similarly, the prolonged presence of humpback and blue whales off the Antarctic Peninsula has been suggested to have impacted body condition in Adelie (*Pygoscelis adeliae*) and Emperor penguins (*Aptendytes forsteri*), which also feed predominantly on krill and small fish [1]. In the unique case of (mammal-eating) killer whales, range expansion into Arctic waters may lead to rising predation on cetacean species that are resident to the Arctic [13,40,73]. Additionally, the presence of killer whales appears to lead to behavioural and distributional changes in all three Arctic cetacean species. Beluga display increased evasive behaviour [73,110] and narwhal spend more time near the coast in tight groups [13,50]. Similarly, bowhead whales spend more time in shallow waters and dense sea ice [63,92].

Secondly, cetacean range changes may also have impacts at a genetic scale, both between populations of the same species and between species

[39,67]. At a population level, gene flow between previously genetically isolated populations of the same species may increase variability within the gene pool and thereby enhance the species' ability to adapt to future (climatic) changes [48,103]. Such flows may be possible because of the opening of new migratory routes due to reduced sea ice concentrations. An example of this would be the opening of the northwest passage linking bowhead whale populations in the Pacific and Atlantic [39]. Contrarily, for some species, certain populations may be unable to shift their distribution due to a combination of habitat preferences and local bathymetry and will, therefore, become genetically isolated [95]. This may result in reduced genetic diversity, as has been observed in pygmy blue whales, which in turn reduced their adaptive capacity [8].

Thirdly, due to their pivotal role as 'ecosystem engineers', shifts in the distribution of various cetacean species is likely to have implications on the wider marine ecosystem. At a large scale, the loss of rorqual whales in some areas may result in reduced productivity and phytoplankton populations as was experienced in the Southern Ocean during the peak of the whaling period [101]. Since marine predators are critical for the management of prey populations, the disappearance of cetaceans from certain regions could also lead to major alterations in community structure and ecosystem function [20,97]. At a smaller scale, the absence of various odontocetes may reduce the foraging opportunities of many marine birds, which rely on toothed whales to drive fish towards the surface while feeding [27]. These are just a few examples and, due to the complexity of marine ecosystems, extensive research will be required to understand and predict the potential changes in trophic interactions following climate-induced shifts in cetacean distribution [85].

Finally, continuous changes in the known distributions of species will make it extremely important to generate legislation to alter existing protected areas to include new ranges [16]. Historically, MPAs were considered the most cost-effective and practical ocean conservation strategy [80]. Yet their lengthy implementation process may render traditional MPAs less effective in future conservation of marine species including many cetaceans [16]. The concept of mobile MPAs (mMPAs) has been put forward as an innovative and dynamic tool to protect mobile and migratory species [65]. Perhaps their implementation, in combination with adoption of adaptive management protocols, could provide a solution to the issue of conserving cetaceans throughout their distributional changes [65,75].

Importantly, this discussion was based on 58 research articles, often focussing on specific populations of certain species. Therefore, the conclusions drawn from the above analysis may not apply to entire species. In addition, the geographical distribution of studies is very uneven, with the majority having been conducted in the northern hemisphere, and many clustered around the continent of North America. No studies meeting our criteria have been conducted on cetacean populations in the South Pacific Ocean or around Africa. Moreover, cetacean families are unequally represented in the climate change literature. Beaked whales were only briefly mentioned in four of the articles, despite being one of the largest cetacean families (22 species). This group is extremely understudied with 20 of the 22 species being listed as data deficient on the IUCN Red List [43]. Finally, the three river dolphin families were not discussed in any of the included papers, even though several species (including the South Asian River dolphins (*Platanista gangetica*), Baji (*Lipotes vexillifer*) and Amazon River dolphin (*Inia geoffrensis*) are listed as (critically) endangered [43]. This uneven distribution of knowledge, both geographically and phylogenetically, highlights a large research gap which should be addressed by future studies.

This review has summarised the direct impacts of two of the primary indicators of climate change in marine environments: increasing/changing SST and reduced/changing sea ice cover on cetacean distribution, habitat and migration. Next to these direct impacts it is crucial to highlight here that there are also a broad range of indirect impacts. For example, reduced sea ice cover in polar regions will lead to increased shipping traffic and therefore noise and chemical pollution and fishing activity in these areas; all of which will influence cetacean

distribution [113,114]. In addition, climate change has already and will continue to result in increased climatic variability [86]. Large-scale climatic phenomenon such as ENSO and Pacific Decadal Oscillation (PDO) have been shown to influence the population dynamics of various marine species including predators at higher trophic levels [96]. Multiple studies have demonstrated a relationship between ENSO conditions and cetacean distribution, reproductive rates and mortality events (e.g. toxic algal blooms) [19,36,87,88]. Research on the cumulative effects of these stressors is key to understand the long term implications of climate change on cetaceans.

Our review shows significant and global impacts of climate change on cetaceans. However, because there are still significant research gaps, and certain families of cetaceans are under investigated, there is an urgent need to further our understanding of these impacts on the overall health of ecosystems. For example, it is unclear how shifts will impact cetaceans roles as 'ecosystem engineers', how climate change might affect prey populations, or species which indirectly depend on whales. Secondly, our research provides key information to increase conservation success. For example, the climate-induced changes in the distribution and movements of cetaceans are important for the development and prioritization of new Marine Protected Areas (MPAs), as well as for adaptation of both local and global policies. Finally, given the important cultural and provisional value of whales for many communities [23], a better understanding is needed on how shifts in distribution and migration patterns will impact both the cultural and economic ecosystem services provided to humans by cetaceans.

## 5. Conclusion

This review has synthesised existing literature on the observed and predicted impacts of climate change on cetacean distribution, habitat and migration in order to highlight research gaps and aid cetacean conservation. We highlight that the distribution of many species of cetacean has already been affected by rising SSTs and reduced sea ice cover and many more will be influenced over the coming decades. Migratory patterns are also shifting, along with the extent of many species' suitable habitat. These changes may benefit certain species, while others will be placed under extreme pressure and may face increased risk of extinction. Existing research on the topic is both extremely limited and unevenly distributed (geographically and phylogenetically). Further research is necessary in order to determine which species and populations are most vulnerable and require the earliest conservation action. Due to the level of uncertainty regarding the coming climatic changes, radical modification of conservation strategies, including the employment of novel tools such as mMPAs and adaptive management will be essential in order to preserve these iconic megafauna.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Supplementary materials

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