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The Effects of Climate Change on Humpback Whales (*Megaptera novaeangliae*): A Review of Current Knowledge

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Abstract

Anthropogenic climate change is transforming marine ecosystems at an unprecedented rate, significantly affecting large migratory species, such as the humpback whale (*Megaptera novaeangliae*). Humpback whales, as other species of baleen whales, require high amount of food resources, and are dependent on productive feeding grounds and environmental cues, providing valuable insights into ecological responses to oceanic changes. This systematic literature review synthesised 39 peer-reviewed studies published from 2000 to 2025 to examine the effects of climate-related environmental changes on humpback whale ecology across global ocean basins. The literature review revealed that rising sea surface temperatures (SST), sea ice variability, and significant climatic oscillations (ENSO, SAM, IOD, PDO, NPGO) constitute over two-thirds of all recorded climate effects affecting the species. These effects were mostly associated with alterations in whale distribution, prey availability, and reproductive success. They have also been associated with changes in migration patterns and abundance. Correspondence analysis confirmed that long-term warming (rising SST) demonstrates a strong link with distributional shifts, whereas short-term heating extremes (marine heatwaves) mostly influence abundance and reproductive success. The spatial research coverage was broad but effort distribution was highly unbalanced. Most studies were focused on the Southern Ocean and North Pacific, whereas the Indian, Atlantic, and Arctic Oceans received less study effort. Distinct regional patterns were evident, with alterations in sea ice impacting the Southern Hemisphere populations and marine heatwaves significantly influencing the population of humpback whales in the North Pacific. These findings highlight the varying sensitivity to climate change of different humpback whale populations around the globe. They emphasise the need for spatially comprehensive evidence to assess vulnerability and inform future initiatives.

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1. Introduction

1.1 Global impacts of climate change on marine ecosystems

Anthropogenic climate change is rapidly altering the world's oceans, significantly impacting marine ecosystems and biodiversity (Calvin et al., 2023; IPCC, 2022). The ocean absorbs over 90% of the excess heat generated by anthropogenic greenhouse gas emissions, and around 25% of the emitted carbon dioxide (Ford et al., 2024; McKinley et al., 2023). This causes significant alterations in both physical and biogeochemical systems. Over the past few decades, the average sea surface temperature (SST) has significantly increased. (Cheng et al., 2019; Garcia-Soto et al., 2021). This has coincided with an increase in the frequency and intensity of marine heatwaves (specific periods of unusually high water temperatures) (Oliver et al., 2018; Smith et al., 2023). Concurrently, ocean acidification (Findlay & Turley, 2021), deoxygenation (Breitburg et al., 2018) and alterations in global salinity patterns (Röthig et al., 2023) are impacting the chemical environment in which marine organisms have developed. These activities influence the circulation, stratification, and nutrient availability in the ocean, therefore altering the productivity and trophic dynamics of marine ecosystems both regionally and globally (Bopp et al., 2013; Laufkötter et al., 2015). Alterations in the timing of phytoplankton blooms can disrupt the connections between predators and prey, a process referred to as trophic mismatch (Edwards & Richardson, 2004). The cascading impacts illustrate the effects of climate-related environment change on marine life.

In addition to warming, fluctuations in large-scale climatic events further intensify oceanic change. Climatic patterns and modes such as the El Niño–Southern Oscillation (ENSO), the Southern Annular Mode (SAM), and the Indian Ocean Dipole (IOD) affect temperature, wind, and precipitation patterns (Kumar et al., 2019). These alterations frequently induce abrupt or periodic fluctuations in marine productivity (Greaves et al., 2020; Hu et al., 2025; Jacox et al., 2015). Future climatic scenarios forecast alterations in the amplitude and frequency of these oscillations, complicating predictions for ecological responses (Alizadeh, 2022; Chen et al., 2024; Chung et al., 2024; Lim et al., 2016).

Numerous marine species depend on consistent environmental signals for feeding, migration, and reproduction; therefore, growing climatic variability threatens the stability of biological cycles and the resilience of populations (Bauer et al., 2020; Kuletz et al., 2024a; Muhling et al., 2020). The ecological consequences of these oceanographic changes affect nearly all marine taxa, but large, long-lived animals with complex life histories are particularly susceptible.

Examining the responses of marine species to habitat alterations is crucial for forecasting future ecosystem changes and establishing conservation policies.

1.2 Baleen whales as indicators of ecosystem health

Baleen whales occupy the top of the food chain (Trites, 2019) and rely on productive, stable oceanic ecosystems for feeding, migration, and reproduction (Moore, 2008). Their ecology and physiology are closely linked to factors such as SST and sea ice extent, making them particularly susceptible to environmental changes (Kuletz et al., 2024b). Due to their mobility and broad distributions, they integrate conditions across large spatial and temporal scales. Therefore, their responses may provide critical insights about significant environmental changes (Gibson et al., 2006; Plön et al., 2024).

Climate change affects whales through multiple, often interconnected pathways. Alterations in ocean circulation patterns, marine heatwaves, and elevated SST may influence the timing and location of prey availability. This would force predators to alter their foraging strategies and migratory patterns (Gulland et al., 2022; Van Weelden et al., 2021; Welch et al., 2023). Variations in sea ice extent influence the accessibility of habitats for many baleen whales and the stability of the food webs upon which they rely (Bester et al., 2017). In addition, ocean acidification can impact lower trophic levels, indirectly affecting the energetic balance and reproductive success of top predators (Doney et al., 2020; Kawaguchi et al., 2013). These processes often act synergistically, intensifying stress and reducing population resilience. Comprehensive research on the population dynamics, distribution, and reproduction rates of whales provides insight into the impacts of climate change on higher trophic levels. Moreover, because these species are charismatic and globally present, they also serve as flagship indicators to raise awareness and funds for conservation initiatives (Nelms et al., 2021; Siddig et al., 2016).

Baleen whales require productive feeding grounds and reliable food sources to sustain energetically demanding migrations and reproductive cycles (Booth et al., 2023; Braithwaite, Meeuwig, & Hipsey, 2015). Changes in ocean conditions that affect prey availability or distribution might lead to nutritional stress, delayed reproduction, or alterations in migratory patterns for whale species (Meyer-Gutbrod et al., 2021; Moore et al., 2022).

Examining how baleen whales respond to environmental variability contributes not only to ecological understanding but also to the management and conservation of

marine ecosystems in a rapidly changing climate. The humpback whale (*Megaptera novaeangliae*) is a species of considerable significance due to its widespread distribution, well-documented migratory patterns and strong dependence on environmental cues and prey availability (Rizzo & Schulte, 2009; Seyboth et al., 2023; Vogel et al., 2023).

1.3 Humpback whale ecology

The humpback whale is a cosmopolitan baleen whale species found in all major ocean basins, ranging from polar feeding grounds to tropical and subtropical breeding areas (Clapham & Mead, 1999). Genetic and photo-identification studies have revealed that the species comprises multiple distinct populations, often associated with specific migratory routes and breeding grounds (Bettridge et al., 2015; Jackson et al., 2014). Figure 1 presents the habitats and migratory corridors of humpback whale populations worldwide (Palacios et al., 2025).

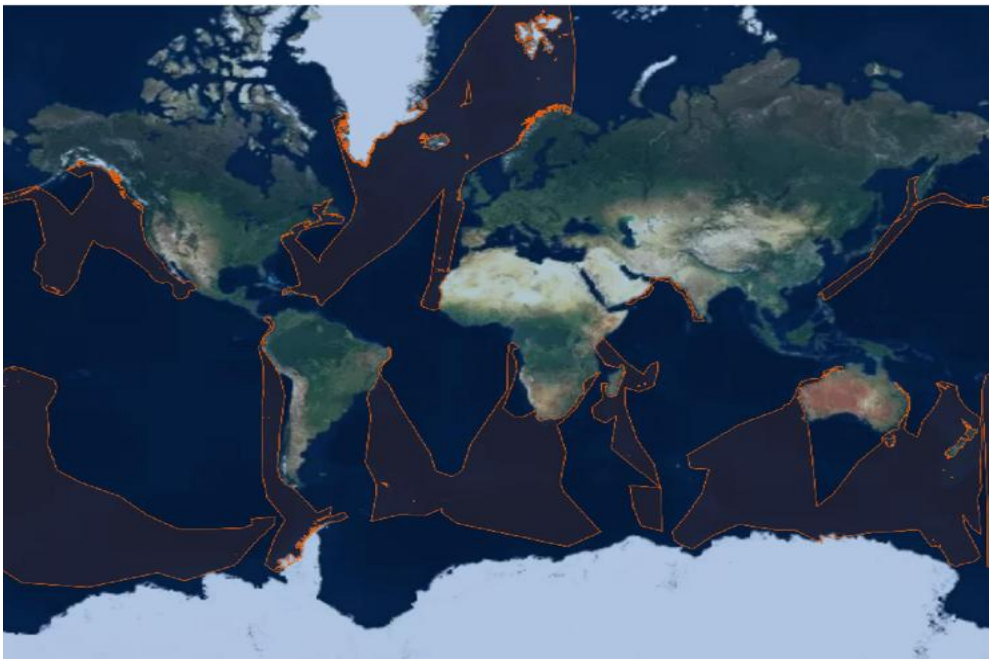

Figure 1 Global distribution and migratory corridors of humpback whales. Data source: Palacios et al. (2025)

Humpback whales have an important function in the ecosystem as a mid- to upper-trophic-level predators, mostly feeding on dense aggregations of small schooling fish and euphausiids (krill) (Witteveen, 2011). The species' broad geographic range and strong reliance on prey availability indicate a strong link between its ecology and oceanic productivity (Meynecke et al., 2021).

Humpback whales undertake some of the longest seasonal migrations of any mammal, travelling up to 8,000 km annually between high-latitude feeding grounds and low-latitude breeding grounds (Bestley et al., 2019; Rasmussen et al., 2007; Russell et al., 2024). These migrations are largely driven by the spatial separation between areas of high prey abundance and areas that provide suitable environmental conditions for calving and nursing (Andrews-Goff et al., 2018; Gales et al., 2009; Rasmussen et al., 2007; Zerbini et al., 2006)

During the summer months, whales intensively feed in productive polar and subpolar regions, accumulating lipid reserves that sustain them during fasting periods, such as during migration and the breeding season (Bierlich et al., 2022; Zerbini et al., 2006). The timing and routes of these migrations are influenced by environmental cues such as SST and prey availability (Millien et al., 2025). Moreover, evidence suggests that humpback whales rely on both immediate environmental information and learned migratory memory, enabling them. This enables them to anticipate seasonal prey peaks and to return to traditional feeding and breeding areas (Millien et al., 2025).

The spatial ecology of humpback whales is strongly associated with oceanographic features that enhance prey aggregation, including upwelling systems, continental shelf breaks, and frontal zones (Friedlaender et al., 2006; Meynecke et al., 2021). In high latitude feeding grounds such as the Southern Ocean, prey availability is closely linked to seasonal cycles in primary productivity (Bamford et al., 2022). In contrast, breeding and calving areas are typically found in warm, shallow tropical waters characterised by low productivity but minimal predation risk for newborn calves (Corkeron & Connor, 1999; Noriega et al., 2024; Rasmussen et al., 2007).

1.4 Humpback whale threats

Humpback whale populations were severely depleted by commercial whaling between the late 1700s and the mid 1900s, when at least 300 000 individuals were killed worldwide (Zerbini et al., 2019). Although the scale of exploitation varied regionally, most populations were driven to critically low levels (Findlay, 2000). Although the species has been protected in the Southern Hemisphere since 1963 (IWC, 1963; Tønnessen & Johnsen, 1982), illegal whaling by certain fleets continued through the 1970s and early 1980s further reducing several populations to dangerously low levels (Gambell, 1993; Ivashchenko et al., 1993). The moratorium on all commercial whaling, implemented by the International Whaling Commission (IWC) in 1986, halted exploitation among member states (Clapham & Baker, 2002).

Following that, some stocks began to show a gradual recovery (Zerbini et al., 2019), and current estimates for the Southern Hemisphere indicate a recovery to about 80% of the pre-whaling abundance of the species (Seyboth et al., 2023). The species' global rebound has led to its current classification as Least Concern on the International Union for Conservation of Nature (IUCN) Red List (Cooke, 2018). Nonetheless, recovery remains uneven subpopulations in the Arabian Sea and parts of Oceania are still considered as Endangered due to their limited size and ongoing anthropogenic pressures (Childerhouse et al., 2008; Minton et al., 2008).

Despite the overall encouraging rebound, humpback whales continue to face numerous anthropogenic threats. Ship strikes are among the most direct sources of human-induced mortality, particularly along heavily trafficked coastal routes and near major ports (Smith et al., 2020; Van Waerebeek et al., 2007). Entanglement in fishing gear remains widespread, leading to injury, chronic stress, and occasionally death, with implications for population growth and individual fitness (Félix et al., 2020; Groom & Coughran, 2012; Santora et al., 2020). Underwater noise pollution from commercial shipping, military sonar, and industrial activity interferes with acoustic communication and echolocation, which are essential for navigation, social interaction, and foraging (Dunlop, 2019; Dunlop et al., 2020; Erbe et al., 2019; Rossi-Santos, 2015). In addition, oil and gas exploration and extraction pose both acute and chronic risks through seismic surveys, pollution, and habitat disturbance (Weilgart, 2007). These cumulative pressures threaten to undermine population recovery, especially where human activity overlaps with key feeding, breeding, or migratory areas.

Beyond these direct human impacts, climate change represents an overarching and multifaceted threat to humpback whales and the ecosystems they depend on. As highly migratory, capital breeding species, humpback whales rely on predictable and productive feeding grounds in high-latitude regions to accumulate lipid reserves that sustain fasting during migration and breeding (Bengtson Nash et al., 2017). Variations in SST, sea ice extent, and primary productivity alter prey availability, disrupting the trophic linkages upon which their energetic balance depends (Bengtson Nash et al., 2023; Klein et al., 2018; Van Weelden et al., 2021). Such changes can manifest as declines in body condition, delayed reproduction and shifts in migratory patterns (Bedriñana-Romano et al., 2022; De Lima et al., 2025; Meynecke et al., 2021; Millien et al., 2025; Seyboth et al., 2023). In tropical breeding areas, warming and ocean acidification may also affect habitat suitability, while altered precipitation and storm regimes could increase calf vulnerability (Kebke et al., 2022)

Overall, the global recovery of humpback whales demonstrates the effectiveness of international conservation efforts. However, the long-term survival of humpback whale populations will rely on the effective mitigation of emerging anthropogenic and environmental threats (Bejder et al., 2016; Zerbini et al., 2019). Understanding and quantifying these pressures is crucial to safeguard the progress achieved since the cessation of commercial whaling and to ensure that positive population trends are maintained in the coming decades. This study aims to review how climate-related environmental changes shape the ecology of humpback whales and to identify emerging patterns that can guide future conservation and management efforts.

1.5 Aims of the study

The goal of this study was to identify and synthesise the documented impacts of climate change on humpback whales based on existing literature. By integrating findings from studies conducted across different ocean basins, this review aimed to provide a comprehensive overview of how environmental variability influences the species' ecology, distribution, and population dynamics.

The specific objectives were to:

- review how climate change has been reported to affect aspects of humpback whale ecology;
- identify which studies have been conducted, on which populations or breeding stocks, and in relation to which climate change drivers; and
- highlight underrepresented geographical areas and research themes to guide future investigations and management efforts.

Ultimately, this study seeks to contribute to a broader understanding of humpback whale vulnerability to climate change and to support the development of informed, spatially inclusive conservation strategies.

2. Methodology

2.1 Systematic literature review

A systematic literature review was conducted in accordance with the guidelines by Siddaway et al. (2019), including both peer-reviewed and grey literature sources. The review protocol was defined beforehand to enhance transparency and reproducibility. Publications on the observed and predicted impacts of climate change on humpback whale ecology were reviewed and analysed. Furthermore,

research gaps, here defined as thematic or geographical areas for which no studies addressing climate change impacts on humpback whales were identified in the screened literature, were identified.

2.1.1 Search strategy

Google Scholar and PubMed served as the primary databases for article searches. The following search terms were used: “Humpback whale body condition and climate change”, “Impacts climate change on humpback whales”, “Climate change and humpback whale diseases”, “Topic or Title = ((climate* AND (change* OR warm*)) OR (temperature* AND (increase* OR ris* OR warm*))) AND (humpback whale*)” and “Climate change impacts on humpback whale health”. Due to time limitations, only the first 50 search results per search term were screened.

The search timeframe was set between the 1st of January 2000 and the 28th of May 2025. Articles published outside of this timeframe, as well as non-English literature, were not considered.

2.1.2 Screening and selection criteria

Initially, publications obtained through the search were imported into Zotero, an open-source reference management software (Digital Scholar, 2025), and duplicates were removed. Subsequently, titles and abstracts were screened for the publications to be either included or rejected in this study according to the following exclusion criteria: (i) not focusing on humpback whales; (ii) not directly evaluating the impacts of climate change; (iii) not presenting new empirical data (i.e., review papers). The full text of all remaining papers was evaluated to confirm eligibility based on the same criteria.

2.1.3 Data extraction

From each eligible publication, the following information was extracted in: (i) type of climate change impact; (ii) humpback whale response variables; (iii) geographical area; (iv) timespan of the study; (v) whale data sampling or observation method; (vi) whether the evidence was observed or predicted; and (vii) reported knowledge gaps and limitations.

In addition to direct climate impacts reported by each study, indirect impacts were included when a study examined an ecological variable (e.g., krill density, prey availability) that is known from the broader literature to be influenced by climate change. For example, studies examining krill density were coded as reflecting sea ice impacts when previous literature establishes that sea ice dynamics influence krill

availability (Atkinson et al., 2019), even if the study did not measure sea ice directly.

2.2 Data organisation

All extracted variables were compiled in an Excel table. For each publication, one document was created summarising the extracted fields; consequently, the documents were uploaded to Atlas.ti (ATLAS.ti Scientific Software Development GmbH, 2025). Each document was then coded under three categories, namely: (1) Climate-change impacts; (2) Humpback whale response variables; and (3) Study area. Additionally, a frequency analysis was conducted by plotting bar graphs for each code group to visualise research emphasis. The three analytical categories (hereafter referred to as code groups in Atlas.ti) were defined as follows:

- Climate change impacts: changing chlorophyll a levels; climate modes (e.g., El Niño Southern Oscillation [ENSO], Pacific Decadal Oscillation [PDO], Indian Ocean Dipole [IOD], Southern Annular Mode [SAM]); delayed spring warming; harmful algal blooms; rising SST; marine heatwaves; ocean acidification; changes in upwelling systems; sea level rise; shifts in prey distribution; southward shift of the Antarctic Circumpolar Current; variability in sea ice extent.
- Humpback whale response variables: abundance; distribution; biotoxin exposure; reproductive success; migration; prey availability.
- Study area: Southern Ocean; Northeast Pacific Ocean; Southwest Pacific Ocean; Northwest Atlantic Ocean; Southeast Indian Ocean; Southeast Pacific Ocean; North Atlantic Ocean; Southwest Atlantic Ocean; Arctic Ocean; East Atlantic Ocean; Global; North Pacific Ocean; Northeast Atlantic Ocean; Northwest Indian Ocean; Northwest Pacific Ocean.

ENSO, SAM, PDO, IOD and North Pacific Gyre Oscillation (NPGO) were classified as climate modes, whereas local oceanographic variables (e.g., SST anomalies, sea ice extent, upwelling changes) and extreme events (e.g., marine heatwaves) were coded in separate categories.

Counting of impacts and study areas was conducted as follows: each study was counted once for every climate change impact it addressed. Consequently, totals across impacts exceed the number of studies (55 impacts across 39 studies). Study

area counts were computed for each area; studies spanning multiple areas were counted only once in each relevant area.

2.3 Spatial visualisation

To visualise study areas across ocean basins, QGIS 3.40.8 (QGIS Development Team, 2025) was used to generate a map. First, the shapefile layer *ne_110m_ocean* from Natural Earth was set as the base layer. Subsequently, the number of studies per area was collected and mapped as a choropleth. A colour-blind friendly purple palette was selected, where darker violet tones indicated higher study counts.

First, the number of studies was summarised at two spatial resolutions: a coarse scale and a fine scale. At the coarse scale, analyses considered broad ocean regions (e.g., Northeast Pacific, Northwest Atlantic, Southern Ocean). Then, at the fine scale, the number of studies per region (e.g., countries, marine parks, breeding and feeding grounds) was analysed. Furthermore, at this scale, the most frequently studied climate impact in each region was identified.

2.4 Co-occurrence analysis

A co-occurrence analysis was performed to evaluate associations between climate impacts and whale responses. As a first step for this, a code–document table was compiled in Atlas.ti from the systematic literature data (n = 39 studies). In this table, climate change impacts and humpback whale response variables were listed as rows, whereas document IDs served as columns. Consequently, each cell listed the presence (1) or absence (0) of a code in each document.

Next, the Atlas.ti export was used to construct a binary code–document matrix in Excel. Specifically, a "impacts × documents matrix A" and a "responses × documents matrix B" (both 0/1) were defined. Subsequently, pairwise co-occurrence counts were computed via matrix multiplication (Excel MMULT), $C = AB\text{^}T$. As a result, the two-way contingency table (impacts × responses) contained, for each cell, the number of distinct studies reporting that impact–response pair.

Additionally, a correspondence analysis (CA) was performed on this frequency table in RStudio 2025.05.1 using packages *FactoMineR* for computation and *factoextra* for visualization (Posit Team, 2025). A symmetric biplot scaling was employed to represent both impacts and responses in the same metric space. Because

both rows (impacts) and columns (responses) are categories rather than continuous measurements, CA was an appropriate choice for detecting and visualising associations. To improve readability and reduce leverage from sparse categories, variables with overall totals < 3 were excluded from the analysis. For plot interpretation, emphasis was placed on (i) distance from the origin, (ii) contributions of categories to each dimension, and (iii) squared cosines (cos^2) as the quality of representation. Consequently, only categories with high contributions and/or $cos^2 \geq 0.20$ were considered for the final analysis.

3. Results

3.1 Overview of the reviewed literature

A total of 150 articles were screened, resulting in the selection of 39 papers for the analysis. The most frequent reason for exclusion of a study was the absence of a direct examination of climate change impacts. Other common exclusion factors were: a focus on species other than humpback whales, and other anthropogenic threats as the target of the studies. To provide an overview of the reviewed studies, a meta-table was created that summarises the study region, climate change impacts, the effects on humpback whales, years of data collection, and references (Table 1). This table offers a structured overview of the thematic and geographic scope of the literature, clarifying which impacts were studied in each ocean basin and which response variables were assessed. Please note that the effects on humpback whales are described in detail in subsection 3.2.

Table 1 *Overview of peer-reviewed articles included in the review, showing region, climate change impacts, affected variables related to humpback whales, study period, and source of information. SST = sea surface temperature*

Study region	Climate change impacts	Effect on…	Years of data collection	Source
Southern Ocean	Variability in sea ice Climate modes	Prey availability	2008-2015	Bengtson Nash et al. (2017)
	Changing chlorophyll a concentrations Rising SST	Prey availability	1890-2012 (historical data) 2000-2100 (future projections)	Tulloch et al. (2019)
	Variability in sea ice	Reproductive success	2004 - 2010	Seyboth et al. (2021)
	Southward shift ACC	Prey availability	Future projections	Tynan & Russell (2008)
	Variability in sea ice	Prey availability	1947 – 1963 (historical data)	Braithwaite, Meeuwig,

			1979 – 1966 (krill data) 1947- 1963 (sea ice data) 1979 - 2007 (sea ice data)	Letessier, et al. (2015)
	Variability in sea ice Rising SST Upwelling changes Changing chlorophyll a concentrations	Prey availability Migration	2009, 2013 - 2016	Millien et al. (2025)
	Variability in sea ice	Reproductive success	2013 – 2020	Pallin et al. (2023)
	Variability in sea ice	Prey availability	May 2009	Nowacek et al. (2011)
	Variability in sea ice	Prey availability	September-October 2015 (tag data) November 2015 - June 2016 (feeding ground data)	Riekkola et al. (2019)
	Variability in sea ice	Distribution	2003 – 2012, 2016 – 2019	Bedriñana-Romano et al. (2022)
	Climate modes	Migration	2010 – 2018	Schall et al. (2021)
	Variability in sea ice	Prey availability Reproductive success Migration	2008 – 2018	Bengtson Nash et al. (2023)
Northeast Pacific Ocean	Marine heatwave Climate modes	Prey availability Reproductive success	2008-2018	Cartwright et al. (2019)
	Climate modes	Prey availability	1993–2012	Fleming et al. (2016)
	Harmful algal blooms (HAB's)	HAB toxin exposure	2007-2011	Lefebvre et al. (2016)
	Marine heatwave	Reproductive success	2001-2019	Frankel et al. (2022)
	Rising SST Changing chlorophyll a concentrations	Abundance Distribution	February and June of 2005 and 2006	García-Morales et al. (2017)
	Variability in sea ice	Prey availability Migration	1988-2018	Avila et al. (2020)
	Marine heatwave Climate modes	Migration	2000 - 2006, 2014, 2015, 2016, 2019, 2020	Pelayo-González et al. (2022)
	Marine heatwave	Prey availability Reproductive success	2015-2021	Ryan et al. (2025a)
	Marine heatwave	Abundance	2002 – 2021	Cheeseman et al. (2024)

North Pacific Ocean	Marine heatwave	Abundance	2002 - 2021	Cheeseman et al. (2024)
Northwest Pacific Ocean	Marine heatwave	Abundance	2002 – 2021	Cheeseman et al. (2024)
Southeast Pacific Ocean	Variability in sea ice	Reproductive success	2004 - 2010	Seyboth et al. (2021)
	Variability in sea ice Rising SST Upwelling changes Changing chlorophyll a concentrations	Prey availability Migration	2009, 2013 - 2016	Millien et al. (2025)
	Climate modes	Distribution	1996-1999, 2013-2014 (Manabi whale data) 2001-2019 (Esmaraldas whale data) 1996-2019 (SST data)	Denkinger et al. (2023)
Southwest Pacific Ocean	Variability in sea ice Climate modes	Prey availability	2008-2015	Bengtson Nash et al. (2017)
	Rising SST	Distribution	1999-2017	Derville et al. (2019)
	Climate modes	Migration Reproductive success	2008 - 2016	Druskat et al. (2019)
	Climate modes	Migration Prey availability	1989-2014	Meynecke & Meager (2016)
	Climate modes	Prey availability	1963 – 2019	Dedden & Rogers (2022)
	Rising SST	Distribution Migration	2000-2020	Fariello et al. (2024)
	Variability in sea ice	Prey availability Reproductive success Migration	2008 - 2018	Bengtson Nash et al. (2023)
Northwest Atlantic Ocean	Variability in sea ice Rising SST	Reproductive success	2004-2018	Kershaw et al. (2021)
	Rising SST	Prey availability Distribution	October 2016	Askin et al. (2017)
	Rising SST	Migration Prey availability	1984-2010	Ramp et al. (2015)
	Delayed spring warming	Migration	1998 – 2018	Pendleton et al. (2022)
North Atlantic Ocean	Rising SST	Abundance Distribution	1986, 1987, 1995, 2001, 2007, and 2009 (whale data collection)	Víkingsson et al. (2015)

			1970-2014 (temperature and salinity) 1980-2014 (capelin abundance data) 2006- 2014 (sand eel abundance data) 1958-2007 (krill abundance data)	
	Rising SST	Distribution	1995 - 2017	Malinauskaite et al. (2022)
Northeast Atlantic Ocean	Rising SST Shifts in prey distribution	Distribution	1990 - 2020	Snell et al. (2023)
Southwest Atlantic Ocean	Variability in sea ice	Distribution	2003- 2012 and 2016 - 2019	Bedriñana-Romano et al. (2022)
	Rising SST Changing chlorophyll a concentrations	Migration	1965-1973 (historical data) 2003 - 2018 (satellite telemetry data)	Horton et al. (2020)
East Atlantic Ocean	Rising SST Sea level rise Ocean acidification	Distribution	2000-2012	Chou et al. (2019)
Arctic Ocean	Variability in sea ice	Distribution	July 2016 (one day on the 29th)	Zein & Haugum (2018)
Global	Rising SST	Distribution	Future projections:until 2100 (Every February and August) Historical data:1985-2001 (Every February and August)	von Hammerstein et al. (2022)
Southeast Indian Ocean	Variability in sea ice	Prey availability	1947 – 1963 (whaling data) 1979 – 1966 (krill data) 1947- 1963 (sea ice data) 1979 - 2007 (sea ice data)	Braithwaite, Meeuwig, Letessier, et al. (2015)
	Upwelling changes Rising SST Climate modes	Reproductive success	Beginning (June) and end of breeding (October) season 2019	Christiansen et al. (2020)
	Climate modes	Prey availability	1963 - 2019	Dedden & Rogers (2022)

3.1.1 Thematic distribution of studies

Across 39 reviewed articles, 54 instances of climate-related impacts on humpback whale ecology were found (i.e., some studies recorded more than one impact). The most frequently reported impacts were rising SST (n = 15; 27.3% of all impacts), variability in sea ice extent (n = 12; 21.8%), and climate modes (n = 10; 18.2%) (Figure 2). Less commonly reported were marine heatwaves (n = 5); changes in chlorophyll a concentrations (n = 4); shifts in prey distribution (n = 2); changes in upwelling (n = 2); delayed spring warming (n = 1); harmful algal blooms (n = 1); ocean acidification (n = 1); sea level rise (n = 1); and the southward shift of the Antarctic Circumpolar Current (n = 1).

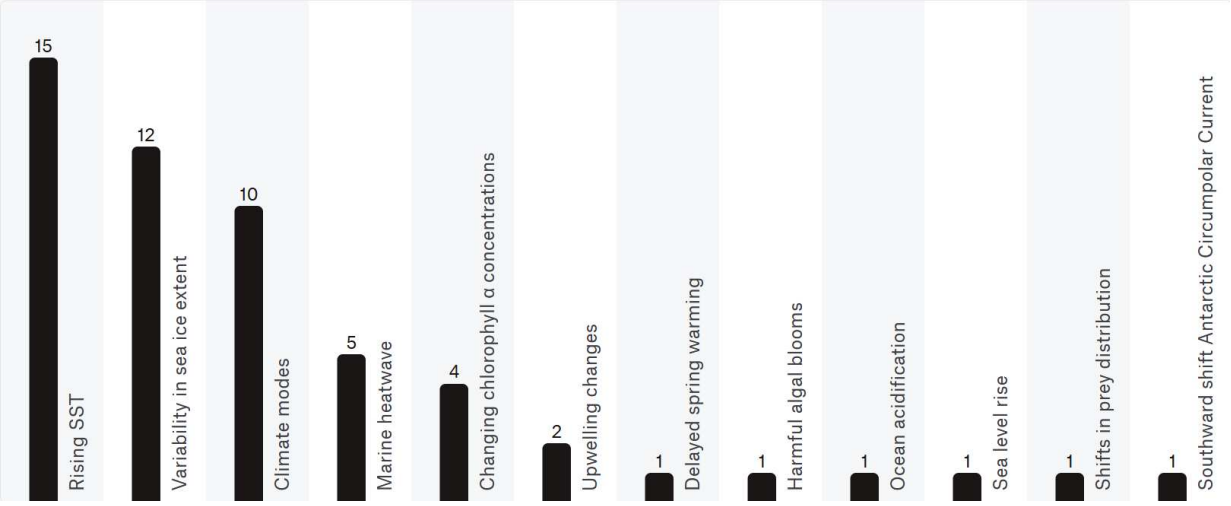

Figure 2. Number of peer-reviewed articles and grey literature referring specific climate change impacts affecting humpback whales (n = 54 impacts across 39 studies).

3.1.2 Distribution of study areas

Study areas spanned all major ocean basins, albeit unevenly represented (Figure 3). The Southern Ocean was the most frequently studied area (n = 12), followed by the Northeast Pacific Ocean (n = 9) and the Southwest Pacific Ocean (n = 6). In contrast, other oceanic areas were notably underrepresented; The Arctic Ocean, North Pacific Ocean, East Atlantic Ocean, Northeast Atlantic Ocean, Northwest Indian Ocean, and Northwest Pacific Ocean each appeared in just one study. One study presented climate change impacts on a global scale without focusing on one specific oceanic region.

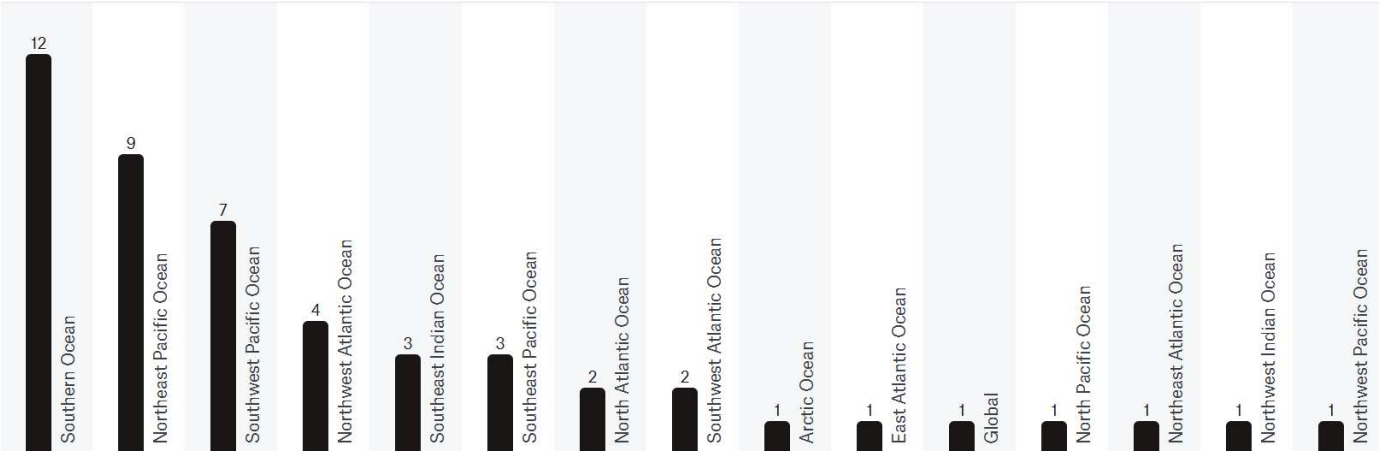

Figure 3. Number of peer-reviewed articles and grey literature per oceanic region that mention a specific climate change impact on humpback whales.

3.1.3 Regional overview

A regional overview of the literature indicates significant spatial variation in the studies on climate change impacts on humpback whales (Figure 4).

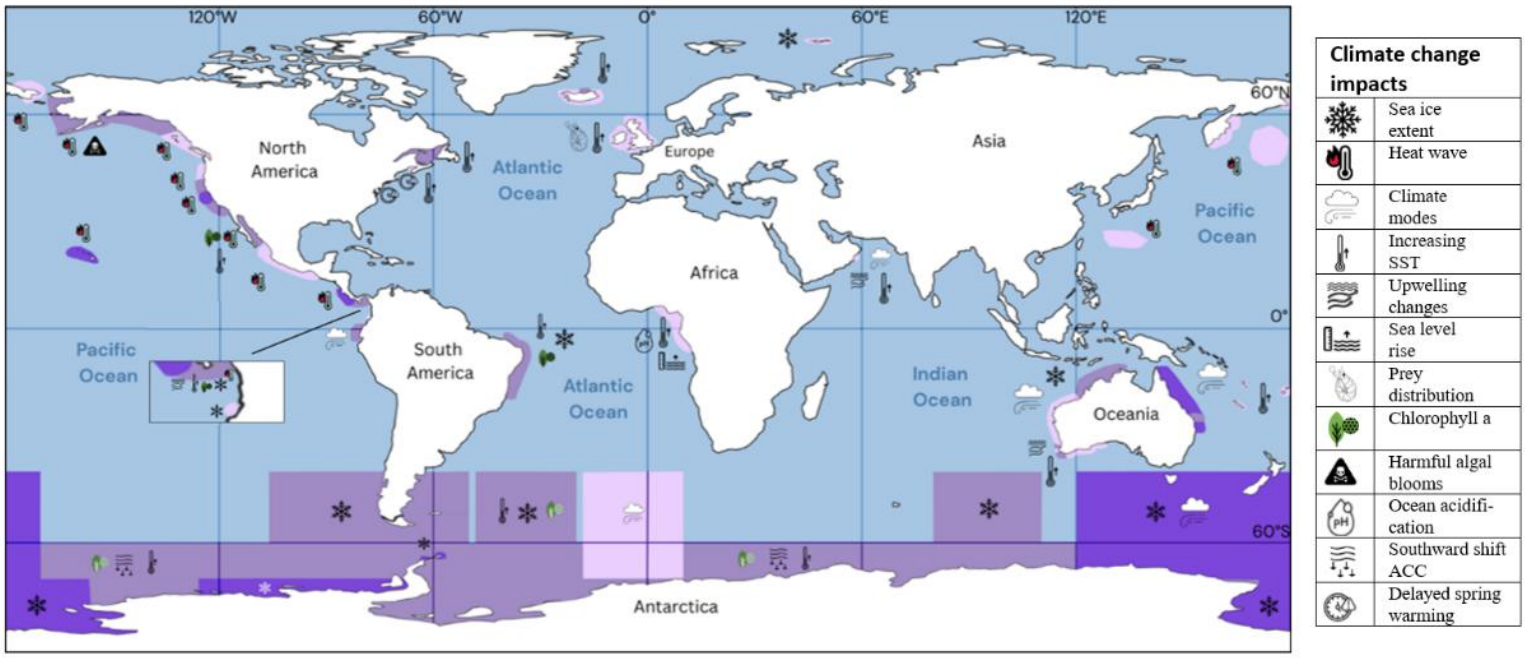

Figure 4. Global distribution of studies on climate change impacts affecting humpback whales. *The map shows the number of studies conducted across different oceanic regions, with darker shades of purple indicating a higher research intensity (light purple = 1 study; darkest purple = 3 studies). Symbols represent the climate change impact most frequently studied in each region (e.g., sea surface temperature, sea ice variability, prey availability).*

In the Southern Ocean (n = 12), sea-ice variability was the most studied climate change impact (n = 9), and prey availability (n = 8) was the most frequently

examined aspect of humpback whale ecology. Studies also examined climate modes (n = 4), chlorophyll-a changes (n = 3), and rising SST (n = 3), with reported effects on reproductive success, migration patterns, and distribution. In the Northeast Pacific Ocean (n = 9), marine heatwaves were the most studied impact (n = 5), followed by climate modes (n = 3). Prey availability (n = 4) and reproductive success (n = 3) were the most reported ecological effects, alongside changes in migration and distribution. In the Southwest Pacific Ocean (n = 7), most studies focused on climate modes (n = 4) and rising SST (n = 2). Prey availability (n = 4) and migration (n = 4) were the most frequently reported effects, with additional observations on distribution and reproductive success. In the Northwest Atlantic Ocean (n = 4), rising SST (n = 3) was the most frequently studied impact, with associated effects on prey availability (n = 2) and migration (n = 2), as well as occasional observations of distribution shifts. In the Indian Ocean (n = 4), studies from the Southeast (n = 3) and Northwest (n = 1) examined changes in upwelling (n = 2), rising SST (n = 2), and climate modes (n = 1). Reported effects primarily related to reproductive success (n = 2) and prey availability (n = 2), with some additional observations on migration. In the Southeast Pacific Ocean (n = 3), most studies examined variability in sea-ice extent (n = 2). No single ecological effect predominated, with studies reporting impacts on reproductive success, prey availability, migration, and distribution. In the North Atlantic Ocean (n = 2), rising SST (n = 2) was the most studied climate impact, with both studies reporting effects on distribution (n = 2). In the Southwest Atlantic Ocean (n = 2), studies examined the impacts of changes in sea-ice extent (n = 1), rising SST (n = 1), and chlorophyll-a levels (n = 1). The most frequently reported effects were on distribution (n = 1) and migration (n = 1). In the Arctic Ocean (n = 1), the single study documented a poleward distribution expansion linked to reduced summer sea-ice cover. In the East Atlantic Ocean (n = 1), the study examined rising SST, sea-level rise, and ocean acidification, reporting effects on humpback whale distribution. In the North Pacific Ocean (n = 1), the study from the Bering Sea investigated the impacts of a marine heatwave on humpback whale abundance. In the Northeast Atlantic Ocean (n = 1), rising SST and shifts in prey distribution were examined, with effects reported on whale distribution. In the Northwest Pacific Ocean (n = 1), the study from the Kamchatka Peninsula and western North Pacific assessed the impacts of a marine heatwave on humpback whale distribution. One global study (n = 1) examined rising SST and its impacts on humpback whale distribution across multiple ocean basins.

3.2 Overview of reported effects of climate change on humpback whales

3.2.1 Overview of main relationships

The CA identified associations between climate change impacts (purple) and ecological responses of humpback whales (red) (Figure 5). A summary of all contributions and cos² values is provided in Appendix A.

The analysis produced four dimensions, of which the first two explained most of the total variation (Dim 1 = 66.1%, Dim 2 = 18.0%; cumulative = 84.1%), and were therefore retained for interpretation. In CA, contribution expresses how strongly a variable influences a given axis, while cos² indicates how well that variable is represented by it. Variables farther from the origin are better represented and have stronger associations, and smaller angles between an impact and a response denote positive relationships (Bock, n.d.).

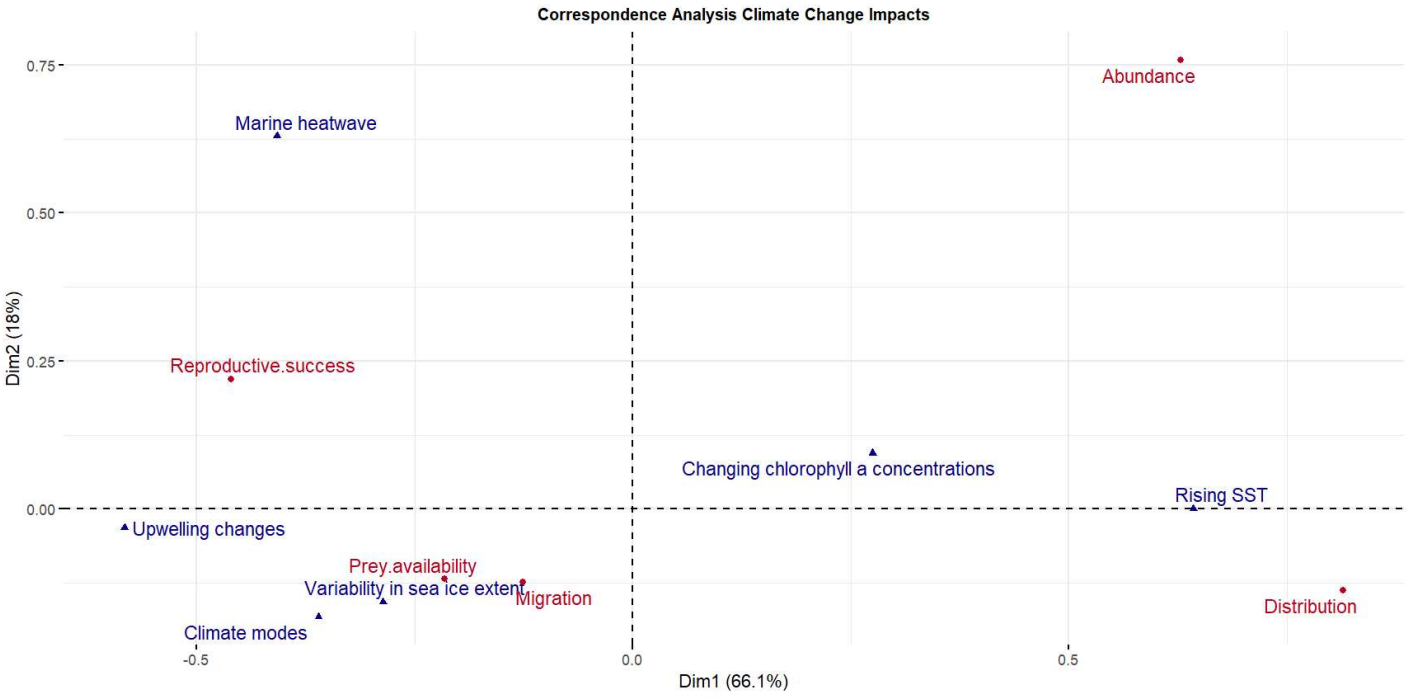

Figure 5. Correspondence analysis biplot showing associations between climate change impacts (purple) and humpback whale response variables (red) across the reviewed studies*. Axes indicate explained inertia (Dim1 = 66.1%, Dim2 = 18.0%).*

Rising SST dominated Dimension 1 (contribution = 58.2 %, cos² = 0.97) and was closely aligned with distribution (contribution = 59.0 %, cos² = 0.93), confirming that long-term ocean warming is consistently linked to spatial shifts in humpback whales. Changes in upwelling systems (cos² = 0.86) and climate modes (cos² =

0.73) also aligned with this axis but lay closer to the origin, indicating a moderate association. Prey availability and reproductive success (both $\cos^2 = 0.63$) were moderately related to the same warming gradient, suggesting that temperature increases were often accompanied by changes in feeding conditions and breeding success across studies. Sea ice variability ($\cos^2 = 0.61$) followed this pattern, reinforcing the overall temperature-driven gradient in which warming and large-scale oceanographic processes correspond with changes in whale distribution, prey dynamics, and reproductive output.

Dimension 2, related to short-term heating extremes, was mainly defined by marine heatwaves (contribution = 75.8%, $\cos^2 = 0.29$). Among the whale responses, abundance (contribution = 62.8%, $\cos^2 = 0.53$) and reproductive success (contribution = 17.0%, $\cos^2 = 0.14$) contributed most strongly to this axis. The sharp angle in which reproductive success and marine heatwaves are positioned suggests that these variables co-occurred more frequently in the literature than marine heatwaves and abundance.

Migration and chlorophyll a concentration (both $\cos^2 < 0.20$) were positioned near the origin, indicating that they were weakly represented on the first two dimensions. This suggests that these variables do not follow the dominant global gradients of warming or thermal extremes identified in this analysis. Instead, their variation is likely driven by more complex or region-specific processes.

3.2.2 Impacts on humpback whale ecology

Rising SST was the most frequently studied climate change impact (n = 15) and was consistently linked to shifts in distribution, abundance, phenology, and habitat use across ocean basins. In the North Atlantic, warmer conditions in the Gulf of St. Lawrence coincided with a decline in calving rates while pregnancy rates remained stable. This suggests reproductive constraints mediated by prey fluctuations under warming conditions (Kershaw et al., 2021). Warmer winters and earlier primary productivity were also associated with earlier arrival and departure of humpback whales from this feeding ground (~1.2 days per year) (Ramp et al., 2015). Around the British Isles, increased strandings and sightings to the north indicated a poleward expansion consistent with rising SST and shifting prey distribution (Snell et al., 2023). In the Pacific basin, rising SST was repeatedly associated with altered prey availability and habitat use. In the Gulf of California, whale abundance was greater during cold, high chlorophyll periods and lower during warm, low productivity phases (García-Morales et al., 2017). Along the Australian east coast, warm

shallow habitats were preferred, but high suitability areas also overlapped with regions of strong anthropogenic pressure (Fariello et al., 2024). In Oceania, encounter rates decreased as SST increased, and by the end of the century, many breeding habitats are projected to exceed optimal temperature thresholds (>28 °C), forcing redistribution toward cooler areas (Derville et al., 2019). At a circumpolar scale, modelling studies predicted that rising SST, together with changing chlorophyll a concentrations, could cause population declines of up to 50% in Pacific Ocean humpback populations by 2100 (Tulloch et al., 2019). Furthermore, Tynan & Russell (2008) projected that warming of approximately 2 °C will drive Southern Ocean fronts poleward, resulting in compressed feeding habitats.

Sea ice variability, the second most frequently studied impact (n = 12), primarily affected prey availability and reproductive success. In the Southern Ocean, several studies demonstrated that fluctuations in sea ice extent influence krill abundance, which in turn drives body condition and reproductive success in humpback whales. On the foraging grounds of breeding stock D, in Western Australia, krill density increased with greater winter sea ice extent in the previous year. Furthermore, body condition was higher following greater sea ice extent over the prior 2–3 years (Braithwaite et al., 2015). Similarly, in breeding stock G, breeding along the west coast of South America, higher pregnancy rates between 2013 and 2020 were linked to increased krill abundance and later spring ice edge retreat (Pallin et al., 2023).At a broader scale, model projections suggest that at ~2 °C global warming, 5–30% of Antarctic sea ice may be lost and Southern Ocean fronts will shift 2–3° poleward, leading to compressed feeding habitats and longer migration routes (Tynan & Russell, 2008). This aligns with findings that whales foraged preferentially near the previous ice edge location and where sea surface height was lowest (Riekkola et al., 2019), indicating a strong dependence on ice edge productivity. Multi-year acoustic monitoring in the Atlantic sector of the Southern Ocean also revealed reduced whale presence during the strong 2015–2016 El Niño, when sea ice concentrations were anomalously low (Schall et al., 2021).

Climate oscillations such as the ENSO, SAM, Indian Ocean Dipole (IOD), and North Pacific Gyre Oscillation (NPGO) were frequently studied (n = 10) for their effects on prey availability and migration. In the Southwest Pacific (breeding substock E1), a study found a strong correlation between stable isotopes of carbon and nitrogen ($\delta^{15}N$ and $\delta^{13}C$) and ENSO/-SAM (Dedden & Rogers, 2022). $\delta^{15}N$ and $\delta^{13}C$ values showed lower and more variable values during El Niño and negative SAM phases, and higher, more stable values during La Niña and positive SAM phases. These trends indicate cyclical shifts in feeding location or prey composition linked

to climate variability (Dedden & Rogers, 2022). During a period of low summer sea ice and strong La Niña/positive SAM, humpback whales were found to have the worst body condition in comparison to other environmental conditions (Bengtson Nash et al., 2017). A male-biased migration was also observed, for the same period, consistent with poor Antarctic feeding and reduced female participation and fecundity (Druskat et al., 2019). Sentinel metrics such as adiposity, female participation in the annual migration, and calf mortality shifted negatively in 2017 during an extreme Antarctic sea ice minimum (Bengtson Nash et al., 2023), while the number of strandings increased under La Niña conditions and when the East Australian Current shifted coastward (Meynecke & Meager, 2016).

Marine heatwaves were examined in five different studies, primarily in the North Pacific. In this area, the 2014–2016 marine heatwave "The Blob" had widespread effects on humpback whale abundance, prey availability, and reproductive success (Cheeseman et al., 2024). Across the North Pacific, abundance rose from approximately 16,900 individuals in 2002 to 33,500 in 2012 before declining 20% by 2021. The heatwave was linked to reduced prey availability and a shift from post-whaling recovery to population decline (Cheeseman et al., 2024). Other studies on The Blob found that in Hawai'i, encounter rates peaked in 2013, while from 2017-2018 encounter rates fell 76.5% (Cartwright et al., 2019). In Kawaihae Bay, whale numbers rose until 2015, then dropped sharply (Frankel et al., 2022). Both studies showed lower abundance and reproductive success following warmer, less productive feeding ground conditions associated with the 2014–2016 heatwave and climate indices (Cartwright et al., 2019; Frankel et al., 2022). In the California Current System, humpback whale diet shifted from krill-dominated during cool, strong upwelling periods to more fish-dominated during warm, negative NPGO/positive PDO conditions, reflecting changes in prey composition linked to the heatwave (Fleming et al., 2016). Similarly, species presence in California rose from 34% to 76% between 2015 and 2021, also coinciding with improving foraging conditions and shifting prey composition after the marine heatwave "The Blob" (Ryan et al., 2025b).

Less frequently studied factors included changes in chlorophyll a concentration (n =4), shifts in upwelling (n = 2), harmful algal blooms (n = 1), delayed spring warming (n =1), ocean acidification (n = 1), sea level rise (n =1). In the Gulf of California, whale abundance and distribution were higher during cold, high chlorophyll periods and lower during warm, low productivity periods, showing the importance of primary productivity for habitat use (García-Morales et al., 2017). In Alaska, exposure to harmful algal bloom toxins was widespread, with 38% of individuals testing positive for domoic acid and 50% for saxitoxin, indicating that warming and sea ice

loss may increase toxin occurrence in feeding areas (Lefebvre et al., 2016). In the Eastern Tropical Atlantic, suitable breeding habitats were primarily determined by SST and sea surface height, with highly suitable areas overlapping zones of heavy cumulative human impacts. Future projections showed that SST and sea level rise may exceed optimal temperature ranges and alter shallow breeding habitats, reducing calm and sheltered areas (Chou et al., 2019).

4. Discussion

4.1 Main findings of the review

This review synthesised 39 studies reporting 54 instances of climate change impacts on humpback whales, revealing three main patterns. First, the majority of the literature addresses impacts associated with ocean warming. Rising SST, changes in sea ice extent, and large-scale climate patterns accounted for over two-thirds of identified impacts. Increasing SST was most frequently linked to shifts in distribution, while sea ice changes and climate patterns were more often associated with prey-related effects influencing reproductive success. Second, prey availability emerged as the primary mechanism mediating climate change impacts on humpback whale ecology across ocean basins. Most studies connected climate variability to changes in prey biomass, composition, or accessibility, which in turn affected distribution, migration patterns, and reproduction. Third, the correspondence analysis is structured along two main gradients: a long-term warming-productivity axis encompassing sea surface temperature, sea ice, prey availability, distribution, and reproductive success, and a short-term thermal extremes axis, where marine heatwaves coincide with changes in abundance and reproductive success.

These patterns indicate that, according to the available literature, humpback whales are primarily affected by climate-driven changes in the spatial and temporal availability of prey, rather than by direct physiological constraints.

4.2 Regional contrasts

A pronounced spatial bias in research efforts represents the second major finding of this review. The Southern Ocean, Northeast Pacific, and Southwest Pacific are heavily represented in the literature, whereas large areas of the Atlantic, Indian, and Arctic Oceans, as well as many tropical breeding regions, are covered by only one or two studies. This imbalance likely stems from factors such as the accessibility of long-term research sites, the historical distribution of marine research groups, and

the availability of monitoring tools, including photo-identification catalogues, telemetry systems, and passive acoustic recorders (Jarić et al., 2015; Tiongson et al., 2021). Regions with established research networks and management interest, such as the Western Antarctic Peninsula, North America, and the eastern Australian migration corridor, have produced multi-decadal datasets that enable the detection of climate impacts (S. M. Bengtson Nash et al., 2023; Bierlich et al., 2022; Cartwright et al., 2019; Cheeseman et al., 2024; Ramp et al., 2015). In contrast, politically complex areas, remote tropical breeding grounds, and parts of the Indian and Atlantic Oceans in the Southern Hemisphere remain understudied, despite the presence of humpback whale populations. (Chou et al., 2019; Tiongson et al., 2021)

This uneven distribution of research substantially affects the confidence with which global conclusions can be drawn. For instance, many strong associations between sea ice dynamics, krill availability, and reproductive success are based on a limited number of Southern Ocean feeding grounds linked to specific breeding stocks. Similarly, most evidence regarding the effects of marine heatwaves comes from the North Pacific "Blob" event. It remains unclear whether similar processes would occur in understudied regions such as the Arabian Sea, parts of the South Atlantic, or the central Indian Ocean.

4.3 Ecological mechanisms and emerging vulnerabilities

Despite these limitations, the reviewed studies collectively identify several climate change impacts that influence humpback whale vulnerability. In high-latitude feeding areas, variations in sea ice, sea surface temperature, and climate patterns consistently altered prey availability, particularly Antarctic krill and small schooling fish (Nowacek et al., 2011; Pallin et al., 2023). These prey-mediated pathways affected body condition, pregnancy rates, calf survival, and migratory participation (Braithwaite et al. 2015; Cartwright et al., 2019; Pallin et al., 2023). Even minor changes in winter or spring conditions can influence reproductive outcomes months later through the food web (Pallin et al., 2023; Schofield et al., 2024). The strong association among rising SST, sea ice variability, prey availability, and reproductive success along the main correspondence analysis axis highlights this shared mechanism.

Short-term extremes, particularly marine heatwaves, introduce additional risks by rapidly reshaping pelagic communities and reducing suitable foraging habitat. North Pacific case studies indicate that such events can reverse previously positive recovery trends, resulting in population declines and reduced reproductive output

within a short timeframe (Cheeseman et al., 2024). Although heatwaves have been studied less frequently than gradual warming or sea ice changes, their strong association with abundance and reproduction in multivariate analyses suggests they may exert a disproportionately large impact when they occur.

One study also identified potential links between climate variability and health or disease risk (Lefebvre et al., 2016). Warmer conditions were associated with increased occurrences of harmful algal blooms and toxin exposure in some feeding areas (Lefebvre et al., 2016). These findings suggest that climate-related ecosystem changes can indirectly influence disease susceptibility, body condition, and immune function, introducing an additional layer of vulnerability beyond energetic constraints. However, health metrics were rarely directly measured in the reviewed literature, highlighting a significant gap for future research.

4.4 Broader ecological and socio-economic implications

Humpback whales act as key ecosystem engineers and potential umbrella species (Roman et al., 2014). By consuming substantial quantities of prey and redistributing nutrients through their movements, they enhance primary productivity and support biodiversity in both feeding and breeding areas (Ratnarajah et al., 2014; Roman et al., 2014) Climate driven declines in whale populations or alterations in migratory patterns can therefore have disruptive consequences for nutrient cycles and food webs in oceanic environments (Doughty et al., 2016; Pearson et al., 2023; Roman et al., 2014).

The socio-economic dimensions of climate impacts on humpback whales are also becoming increasingly evident. Many coastal communities depend on the predictable presence of whales for activities such as whale watching (Castro et al., 2022; Sousa et al., 2023). Changes in migration patterns and distribution, can result in mismatches between traditional operating seasons and the actual presence of whales (Meynecke et al., 2017). In regions with limited scientific data, these economic signals may serve as early indicators of climate-driven ecological change. Integrating local knowledge and industry observations with scientific monitoring could enhance the detection of emerging impacts and inform management strategies that support both conservation and local livelihoods.

4.5 Knowledge gaps and future research

This review identifies several critical gaps. Geographically, the most pressing need is for systematic monitoring in underrepresented areas, especially the Indian Ocean, South Atlantic, parts of the North Atlantic, and tropical breeding regions. Without more balanced coverage, global assessments of climate vulnerability will remain disproportionately influenced by a few well-studied regions. Thematically, there is limited research on specific climate drivers, such as ocean acidification, sea-level rise, and interactions among multiple stressors.

Methodologically, future research would benefit from integrating multiple data sources, such as telemetry, acoustics, stable isotopes, prey surveys, and environmental models, within consistent analytical frameworks. Long-term collaborations across ocean basins, aligned with initiatives such as Protecting Blue Corridors, could help standardize metrics and enhance the comparability of findings across different populations and regions.

4.6 Limitations of this review

Several limitations should be considered when interpreting the findings of this review. First, only 39 studies were included, partly due to time constraints and the requirement that climate impacts on humpback whales be explicitly or implicitly examined. As a result, some relevant literature may have been excluded, and the synthesis does not provide a comprehensive account of all potential climate influences on the species. Second, in some cases, climate impacts were coded indirectly. For example, studies examining krill density or prey availability were interpreted as reflecting sea-ice or temperature impacts based on established relationships in other literature. While this approach captured key ecological pathways, it introduces an additional layer of interpretation. These methodological decisions are detailed in the methodology section and should be considered when comparing impact frequencies.

Third, classifying studies under specific impact types was challenging because many climate variables are interrelated. Rising SST, sea ice loss, and changes in climate patterns often occur simultaneously. Assigning a study to a primary impact category therefore simplifies complex environmental realities. Fourth, this review did not conduct a formal meta-analysis of effect sizes due to the diversity of study designs and metrics, which limited quantitative synthesis. The correspondence analysis and co-occurrence summaries should therefore be regarded as tools for

visualizing broad relationships rather than as precise estimates of effect strength. Despite these limitations, the structured categorization of impacts, responses, and regions provides a clear overview of current knowledge and highlights areas where evidence is stronger or weaker.

5. Conclusion

This review demonstrates that climate change is influencing humpback whale ecology, primarily through temperature driven shifts in prey availability. The strongest evidence is found in populations from the North Pacific, North Atlantic, and Southern Ocean, where changes in SST, sea ice extent, and marine heatwaves have coincided with alterations in distribution, migration patterns, and reproductive success.

However, global understanding of these impacts remains limited. Research has primarily concentrated on a few regions, while large areas of the Atlantic, Indian, and Arctic Oceans, as well as many tropical breeding grounds, lack systematic monitoring.

Given these uncertainties, the long-term resilience of humpback whales will depend on adaptive conservation strategies supported by ongoing monitoring and research. Management approaches that consider shifting habitats, prey dynamics, and migratory corridors, including dynamic or mobile protected areas, will be essential for ensuring the continued recovery and persistence of humpback whale populations in a rapidly changing ocean.

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Appendix

Appendix A. Correspondence Analysis Outputs

Figure A1

Binary table row contributions of climate change impacts to each CA dimension

	Dim 1	Dim 2	Dim 3	Dim 4
Changing chlorophyll a concentrations	3.368613	1.456092e+00	76.0294760	7.99567140
Climate modes	12.516528	1.187700e+01	3.5368810	17.14170789
Rising SST	58.220584	2.966699e-04	8.4047736	3.68684549
Marine heatwave	8.630717	7.580257e+01	2.5233220	0.03488182
Upwelling changes	7.547939	8.611345e-02	0.2515422	30.62217212
Variability in sea ice extent	9.715620	1.077793e+01	9.2540052	40.51872127

Note. Output from the correspondence analysis in R (FactoMineR). Values show each impact's contribution (%) to the variance explained by the four dimensions.

Figure A2

Binary table column contributions of humpback whale responses to each CA dimension

	Dim 1	Dim 2	Dim 3	Dim 4
Abundance	11.695582	62.789338	15.4669483	3.798132
Distribution	58.986569	6.257897	14.8029753	1.202559
Migration	1.654152	5.861691	35.5116125	35.097544
Prey.availability	7.257353	8.054352	0.7688502	51.106945
Reproductive.success	20.406344	17.036722	33.4496136	8.794820

Note. Dimensions 1–2 explained 84.1 % of total variance and were retained for interpretation (see Section 3.3).

Figure A3

Row cos² values of climate change impacts per CA dimension

	Dim 1	Dim 2	Dim 3	Dim 4
Changing chlorophyll a concentrations	0.1724299	2.024062e-02	0.792205057	0.0151243802
Climate modes	0.7321608	1.886700e-01	0.042115023	0.0370542242
Rising SST	0.9692480	1.341236e-06	0.028482517	0.0022681633
Marine heatwave	0.2902939	6.923862e-01	0.017276577	0.0000433562
Upwelling changes	0.8622137	2.671351e-03	0.005849131	0.1292657909
Variability in sea ice extent	0.6063317	1.826621e-01	0.117561070	0.0934451043

Note. Output from the correspondence analysis in R (FactoMineR). Cos² values indicate the quality of representation of each variable on the respective dimension. High cos² (> 0.20) denotes variables that are well represented and closely associated with the main gradients in the biplot.

Figure A4

Column cos² values of humpback whale response variables per CA dimension

	Dim 1	Dim 2	Dim 3	Dim 4
Abundance	0.3650788	0.53226036	0.09827961	0.0043812283
Distribution	0.9253704	0.02666025	0.04727216	0.0006971557
Migration	0.1405188	0.13522456	0.61407807	0.1101785265
Prey.availability	0.6316375	0.19036791	0.01362151	0.1643730570
Reproductive.success	0.6343885	0.14383004	0.21167776	0.0101036465

Note. Cos² values measure how well each response variable is represented on the CA axes. Higher values indicate stronger alignment of the variable with the respective dimension's pattern.