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An update on the implications of climate change for cetaceans - with a particular focus on the Mediterranean Sea.

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Abstract

Climate change interacts with cetaceans, their prey and their habitats in numerous ways and there is growing evidence that cetacean populations are responding to the changes caused by climate change. This review takes into account the most recent scientific literature to provide an update for the IWC Scientific Committee and looks at the Mediterranean in particular as a case study.

Introduction

Ocean warming progressed faster over the past century than at any other time since the end of the last deglacial transition (IPCC, 2021). In addition, ocean acidification has led to unusually low (i.e. increasingly acidic) surface open ocean pH levels in recent decades when compared to the last 2 million years (IPCC, 2021). Both processes are projected to continue, as is ocean deoxygenation (IPCC, 2021). Climate change will also affect ocean circulation, stratification, sea ice cover, salinity, and large-scale atmospheric and ocean modes (IPCC, 2021). The continued mass loss of both the Greenland and Antarctic Ice Sheets will contribute to global sea level rise over the 21st century (IPCC, 2021). Even under large net negative CO_2 emissions, it will take several centuries or even millennia for global mean sea level to reverse course (IPCC, 2021). The Arctic Ocean will likely be practically ice-free for the first time during the seasonal ice minimum before 2050 under all scenarios, a state that might become the new normal by 2100 under continued high greenhouse gas emissions (IPCC, 2021).

Many of these impacts will pose major challenges to marine organisms and ecosystems around the globe and may push some of them to or beyond their capacity to adapt or acclimate.

There is a swifty growing scientific literature that considers the ways that climate change may be affecting cetaceans and far more information is now available than when international fora started to consider this matter and determined that there was not enough information to make sensible predictions for cetaceans (IWC, 1997).

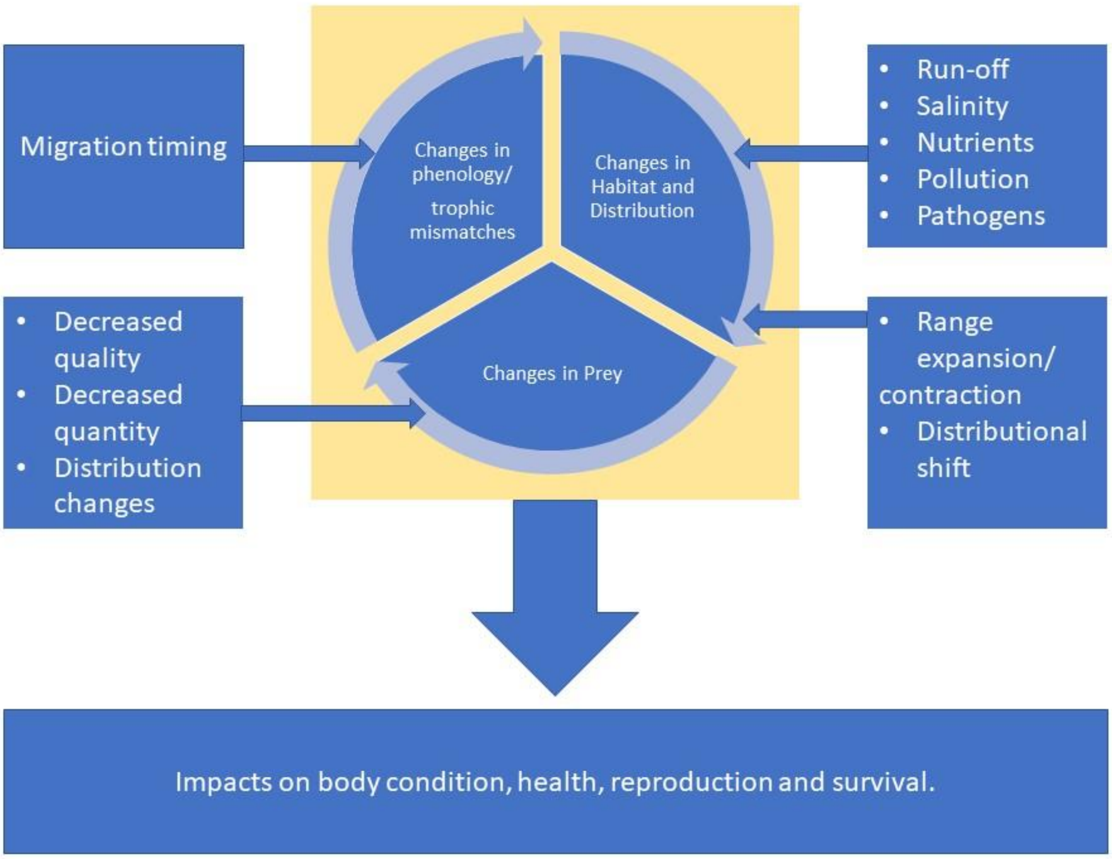
Climate change affects cetaceans both directly and indirectly, the latter by affecting their prey, habitat, food webs and ecosystems. Among the multitude of impacts now observed and predicted are:

- shifts in cetacean distribution and abundance;
- loss of habitat;
- altered species and trophic interactions;
- altered inter- and intraspecific competition;

- reduced reproductive success;
- changes in phenology and migrations;
- relocations of feeding and/or breeding grounds;
- trophic mismatches;
- increased exposure to pollution, pathogens, extreme weather events, marine heatwaves, and toxic algal blooms;
- changes in behaviour; and
- increased stress levels and higher susceptibility to diseases or other anthropogenic stressors[1].

Climate change impacts can also negatively affect the health, body condition, immune system, and survival of individuals and reduce the adaptive capacity and genetic variability within populations or species.

Here we present an overview of the main observed and projected effects of climate change on cetaceans in the scientific literature considering the latest publications and taking a particular look at the situation in the Mediterranean Sea, grouping the effects according to the causal mechanisms they have been attributed to.



[1] A spreadsheet of published works describing and categorizing observed and predicted impacts of climate change on cetaceans is available from the authors.

Figure 1: Climate change and cetaceans - some of the main interlinkages and key factors based on the available scientific literature.

Methods

Literature surveys were conducted using Web of Science and Google Scholar and a range of standard key words.

Impacts of ocean warming

The world's oceans have absorbed over 90% of the excess heat accumulated in the Earth system since preindustrial times (IPCC, 2021). Past greenhouse gas emissions mean that the global oceans will continue to warm, with likely ocean warming over the rest of the 21st century ranging from 2-4 (SSP1-2.6) to 4-8 times (SSP5-8.5) the 1971-2018 change (IPCC, 2021). Indeed, the ocean heat content in 2022 again broke the pevious year's record as the warmest year on record (Cheng et al., 2023). These temperature changes will be irreversible on centennial to millennial time scales (IPCC, 2021).

In addition to gradual ocean warming, extreme temperature events, so-called marine heatwaves, are increasing. They have approximately doubled in frequency since the 1980s and are projected to increase both in frequency and intensity, particularly in the tropical ocean and the Arctic (IPCC, 2021).

The projected increase in marine heatwaves will add additional pressures to many coastal and marine ecosystems, with the potential to cause adverse effects on marine organisms, including habitat-forming species, and changes in primary production, shifts in species compositions, abundance and distributions, and toxic algal blooms (e.g., Smith et al., 2023; Garrambou et al., 2022; Gurgel et al., 2020; Smale et al., 2019; Cavole et al., 2016; Wernberg et al., 2016 & 2013).

Climate projections show that the Mediterranean region will be among the most affected regions in the world and has been termed a primary climate change "hot-spot" (IPCC, 2022; Giorgi, 2006). Future annual and summer warming rates are projected to be 20% and 50% larger than the global annual average, respectively (IPCC, 2022). Basin-wide, annual mean temperatures are now already 1.5°C above the pre-industrial level (IPCC, 2022).

Marine heatwaves have become more frequent, intense, severe, and spatially extended over recent decades in the Mediterranean Sea (Darmaraki et al., 2019a; Oliver et al., 2018), and this trend is projected to continue (IPCC, 2022). By 2100 and under the RCP8.5 greenhouse gas emmission scenario[2], models project at least one long-lasting marine heatwave every year up to 3 months longer, about 4 times more intense and 42 times more severe than today's events (IPCC, 2022). Their occurrence is expected between June and October, and at peak, they will affect the entire Mediterranean Basin (Darmaraki et al., 2019b).Alongside direct effects on cetaceans, many of the changes to the bio-chemical and physical properties of sea water are projected to have profound impacts on marine ecosystems, biodiversity, productivity, ecology, and species assemblages, as well as organisms on various levels of the trophic web. It is likely that these effects may ultimately, and

[2] The warming scenario known as "RCP8.5" has been widely used in projections and is a high-emissions scenario often referred to as "business as usual".

indirectly, affect cetaceans as well. An overview of the projected and already observed effects on cetaceans around the globe, both direct and indirect, are discussed below, including some examples, and some of the key linkages are shown in Figure 1.

Already, ocean warming, acidification, deoxygenation, sea level rise and other consequences of climate change act in concert to alter marine environments and life as we know them. Ocean warming alone might cause changes in primary production and the composition of phytoplankton blooms (e.g., IPCC, 2007) with possible consequences reverberating through entire food webs (e.g., Gambaiani et al., 2009; Molinero et al., 2007 & 2005; Voarino, 2006; Mercado et al., 2005; Edwards & Richardson, 2004; Fernandez de Puelles et al., 2004; Hiscock et al., 2004; Béthoux et al., 2002). It might change species abundances (e.g., van Weelden et al., 2021; Bryndum-Buchholz et al., 2019; Elliot & Simmonds, 2007; Learmonth et al., 2006) and ecosystems' structure and function (e.g., Bryndum-Buchholz et al., 2019), and lead to shifts in species' distributions and changes in the suitability of habitats (e.g., van Weelden et al., 2021; Albouy et al., 2020; Pinsky et al., 2020; Pecl et al., 2017; Poloczanska et al., 2016; Polovina et al., 2011; Learmonth et al., 2006; MacGarvin & Simmonds, 1996), cause local or global extinctions (Grose et al., 2020), alter species assemblages and community structures as well as ecological/trophic interactions and competition (e.g., IPCC, 2001b), and lead to food web shifts (Gambaiani et al., 2009; Harris & Tyrrell, 2001; Frank et al., 2005; Galil et al., 2007).

Rising water temperatures are also expected to encourage toxic algal blooms and amplify the propagation of pathogens and diseases, as well as thermophilic and invasive species (e.g., MedECC, 2020; UNEP/MAP, 2017; UNEP-MAP-RAC/SPA, 2010, Gambaiani et al., 2009). The latter can lead to novel competitions with indigenous species and might cause food web shifts (Gambaiani et al., 2009).

In the Mediterranean Sea, the composition of most of the present marine and coastal ecosystems is expected to change under continued warming and there will be a greater risk of species extinctions – especially those with a restricted climatic distribution, those that require highly specific habitats, and/or small populations which are naturally more vulnerable to modifications in their habitats (UNEP/MAP, 2017).

Additionally, marine heatwaves will contribute to mortality events, and rising ocean temperatures might promote the displacement of ecotypes and shifts in ecosystem functioning (MedECC, 2020). There will likely be changes in the composition, distribution, and abundance of fish populations because of ocean warming, with more warm-water species and a decrease in fish size (UNEP/MAP & Plan Bleu, 2020).

Cetaceans have been observed and predicted to shift their distributions both in direct response to ocean warming and as a response to range shifts in their prey (e.g., Snell et al., 2023; van Weelden et al., 2021; Grose et al., 2020; Lambert et al., 2014; MacLeod, 2009; Learmonth et al., 2006). One example is provided by bottlenose dolphins (*Tursiops truncatus*) off Corsica, which were observed to shift their distribution following changes in both the distribution and abundance of their prey species (Dhermain, 2003). Endangered Maui dolphins (*Cephalorhynchus hectori ssp. maui*) in New Zealand have responded to marine heatwaves with marked range shifts (Baker et al., 2018). As such extreme events increase in intensity and frequency (Salinger et al., 2019), the future recovery of Maui dolphins may be impeded (Grose et al., 2020).

A study modelling the impacts of ocean warming on 78 cetacean species found that the species ranges of 88% of them may be affected (MacLeod, 2009). These changes are anticipated to be unfavourable for 47% of them – and put at least one geographically isolated population of the species at risk of extinction for 21% of them (MacLeod, 2009). It is expected that cetaceans with ranges restricted to non-tropical waters and a preference for shelf waters (MacLeod, 2009), as well as Arctic cetaceans (e.g., van Weelden et al., 2021; Hamilton et al., 2019; Vacquié-Garcia et al., 2018; MacLeod, 2009; Learmonth et al., 2006; Heide-Jogensen & Leidre, 2004) will be at greater risk of such impacts. Similarly, warming sea temperatures are going to pose a particular challenge for species or populations whose distributions are already close to or at the edge of their preferred temperature range (MacLeod, 2009).

Additionally, distributional shift may not always be possible, for example when barriers restrict the movement of cetaceans or their prey, as might be the case in in semi-enclosed sea or due to discontinuities in their preferred seabed bathymetry (e.g., MacLeod, 2009; Simmonds & Isaac, 2007; Learmonth et al., 2006). The Mediterranean fin whales' (*Balaenoptera physalus*) future ability to adapt to warming is of concern, for example, as their only know prey species, Northern krill *(Meganyctiphanes norvegica)* currently lives at the thermal limit of its distribution (van Weelden et al., 2021). If *M. norvegica* proves unable to shift its range due to land barriers, climate change might lead to strong declines in its abundance and potentially drastic reductions in food availability for Mediterranean fin whales (van Weelden et al., 2021).

Cetaceans have also been both observed and projected to lose proportions of their habitat, experience reduced quality of habitat and suffer range contractions (e.g., Evans & Waggitt, 2020; Tulloch et al., 2019; Cañadas & Vázquez, 2017; Ainley et al., 2012; Tynan & Russel, 2008; Heide-Jorgensen & Leidre, 2004). Examples include a predicted northward range contraction in common minke whales (*Balaenoptera acutorostrata*) in the Eastern North Atlantic due to reduced availability of suitable habitat and summer feeding grounds in UK and Irish waters, a drop in in the occurrence of white-beaked dolphins (*Lagenorhynchus albirostris*), and a northward range contraction with significantly reduced summer occurrences in Cuvier's beaked whales (*Ziphius cavirostris*) in the same area by 2090 (Lambert et al., 2014). Short-beaked common dolphins (*Delphinus delphis*) in the Alboran Sea might suffer a reduction in suitable habitat followed by a predicted reduction in their density from east to west over the next 100 years (Cañadas & Vázquez, 2017).

On the other hand, poleward range expansions have been observed, for example, in humpback (*Megaptera novaeangliae*), fin, and common minke whales (Brower et al., 2018, Storrie et al., 2018), killer whales (*Orcinus orca*) (Stafford, 2019; Higdon et al., 2012), and blue (*Balaenoptera musculus*), and sperm whales (*Physeter macrocephalus*) (Storrie et al., 2018). Striped dolphins (*Stenella coeruleoalba*) are also predicted to experience a northward range expansion and an increase in summer occurrence in the UK (Lambert et al., 2014). Bryde's whales (*Balaenoptera edeni)* are also predicted to gradually expand their distributions poleward with long-term ocean warming and prey range shifts, and have, indeed, already been increasingly observed off Southern California in autumn (Kerosky et al., 2012; MacLeod, 2009;).

Serious concerns have been raised regarding possible trophic mismatches arising from climate change-driven effects (Elliot & Simmonds, 2007). There are increasingly more observations of changes in the timing and duration of migrations linked to warming sea temperatures and resulting changes in the abundance, availability, or distribution of prey (e.g., van Weelden et al., 2021; Charif et al., 2020; Nunny & Simmonds, 2019; Ramp et al., 2015; Ezer et al., 2013; Carter & Nielsen, 2011; Rugh et al., 2001). One example is the 1-week delay in the south-bound migration of grey whales (*Eschrichtius robustus*) in the eastern North Pacific compared to before 1980 (Rugh et al., 2001). Humpback and fin whales in the Gulf of St. Lawrence have both shifted their arrival at their summer feeding grounds at a previously undocumented rate of 1 day per year between 1984 and 2010 (Ramp et al., 2015). Similar shifts have since been recorded for blue whales in California and the eastern tropical Pacific: they arrived more than 1 month earlier in 2018 and 2017 compared to 1988 and 2008 in the two locations, respectively (Avila et al., 2020, Szesciorka et al., 2020). Such phenotypic plasticity in response to ocean warming could be considered signs of hope; however, it is unclear whether whales will be able to continue adapting their migrations under the projected rates of changes (Ramp et al., 2015).

There are indications that feeding and/or breeding grounds might undergo relocation under current warming rates (e.g., Meyer-Gutbrod et al., 2018; Thomas et al., 2016; Hamilton et al., 2007; Shelden et al., 2004). Grey whale mothers, for example, have been increasingly observed with new-born calves prior to their arrival at the breeding grounds (Thomas et al., 2016, Shelden et al., 2004). It is suspected that warmer sea surface temperature anomalies, along with ocean warming have led to this phenomenon, though other factors might be involved (Shelden et al., 2004). It remains unclear if the rougher waters or other factors outside the breeding grounds might reduce calf survival rates (Grose et al., 2020).

For some species, such as humpback whales in Oceania, breeding grounds are projected to become unsuitably warm by the end of the 21st century (Derville et al., 2019). However, the whales' apparent plasticity in habitat use and a projected availability of alternative suitable habitat support a certain adaptive capacity in this species in the face of ocean warming, even as distributional shifts might be restrained by philopatry (Derville et al., 2019).

Ocean warming can reduce cetaceans' reproductive success and conception rates (Grose et al., 2020; Cartwright et al., 2019; Seyboth et al., 2016; Meyer-Gutbrod et al., 2015; Gambaiani et al., 2009). This has been observed, for example, in North Atlantic right whales (*Eubalaena glacialis*) (Meyer-Gutbrod et al., 2015) and sperm whales (Whitehead, 1997).

On an individual level, ocean warming may additionally affect cetaceans' performance, survival, and body condition (e.g., Burek et al., 2008; Politi & Bearzi, 2004; Politi et al., 2000), as well as behaviour (e.g., Bearzi, 2002; Bearzi et al., 1999; Politi, 1998). One example is changes in cetacean feeding strategies and time and energy allocation (e.g., foraging vs. socializing) with potential drastic consequences on their health, immune systems, and reproductive success following climate-driven reductions in prey availability (Bearzi, 2002; Agardy, 1996; Bräger, 1993; Smith & Whitehead, 1993; Shane, 1990; Northridge, 1984). This has been observed in bottlenose dolphins in the northern Adriatic Sea (Bearzi, 2002; Bearzi et al., 1999; Politi, 1998; Valiela, 1995).

Climate-driven decreases in prey availability, quality, and abundance (Gambaiani et al., 2009; Geraci & Lounsbury, 2002; Simmonds & Mayer, 1997; Aguilar &, Raga 1993; Aguilar et al., 1991) and also increases in toxic algal blooms due to ocean warming can have significant health impacts and lead to increased mortality rates in cetaceans (e.g., Häussermann et al., 2017; Lefebvre et al., 2016; Gambaiani et al., 2009; Geraci & Lounsbury, 2002). Mortality events following toxic algal blooms have been observed, for example, in grey whales off Alaska (Gulland et al., 2005; Moore et al., 2003;

Grebmeier & Dunton, 2000), and increased mortality following climate-driven decreases in prey in striped dolphins in the eastern Mediterranean Sea (e.g., Simmonds & Mayer, 1997; Aguilar &, Raga 1993; Aguilar et al., 1991). More frequent and severe marine heatwaves might also cause dramatic declines in cetacean prey species (Arimitsu et al., 2021; Barbeaux et al., 2020; Brodeur et al., 2019), and have been linked to declines in abundance and calf production rates (Arimitsu et al., 2021; Suryan et al., 2021; Neilson & Gabriele, 2019), and possibly whale mortality events (Savage, 2017).

Similarly, ocean warming can increase the exposure of cetaceans to pollutants and pathogens (Gulland et al., 2022; Gambaiani et al., 2009; Burek et al., 2008; Learmonth et al., 2006). Warming-induced reductions in prey availability might lead to a higher exposure of cetaceans to contaminants stored in their blubber when mobilized during times of starvation – which, in turn, could impact their reproductive, endocrine, and immune systems (Ross et al., 2000; Aguilar et al., 1999; Aguilar & Borrell, 1994; Fuller & Hobson, 1986).

Reduced prey availability caused by ocean warming is expected to increase cetaceans' vulnerability to diseases, especially in those that live at the limit of their thermal distribution (Lafferty et al., 2004). Such vulnerability might be exacerbated because of reduced immune functions following decreased prey availability and increased energy expenditure for hunting (Gambaiani et al., 2009; Bearzi, 2002; Aguilar & Raga, 1993).

It is also expected that ocean warming could alter cetacean species compositions, trophic interactions and (inter-specific) competition (van Weelden et al., 2021). Examples include a potential colonization of the eastern Mediterranean by *Stenella* and *Mesolpodon* species if ocean warming in the eastern Atlantic and western Mediterranean around the Strait of Gibraltar removes a potential barrier to species ranges (MacLeod, 2009). This would likely have consequences for ecological competition (MacLeod, 2009). MacLeod and colleagues (2008) observed increased inter-specific ecological competition and altered niche partitioning in short-beaked common and white-beaked dolphins in Scottish waters.

Especially due to distributional shifts, ocean warming might also have impacts on genetic diversity and adaptive capacities of cetaceans (e.g., van Weelden et al., 2021, Charif et al., 2020; Cartwright et al, 2019; Miralles et al., 2016; Attard et al., 2015; Ramp et al., 2015; Salvadeo et al., 2015; Bailleul et al., 2013; Heide-Jorgensen et al., 2012; Burek et al., 2008; Elliot & Simmonds, 2007). Gene flow between previously isolated populations of the same species may increase the genetic variability within the gene pool and enhance a species' adaptive capacity regarding future changes (Kelly & Phillips, 2016; Tigano & Friesen, 2016). This might happen, for example, if new migratory routes open as a result of lower sea ice concentrations – which could become the case with the Northwest Passage, linking bowhead whale populations in the Pacific and Atlantic (Heide-Jorgensen et al., 2012). On the other hand, the mixing of species or previously isolated populations of the same species could also result in a loss of genetic diversity, a loss of uniqueness between populations or species, new hybridisations, and the introduction of novel pathogens and/or parasites (ACCOBAMS, 2021; van Weelden et al., 2021; Miralles et al., 2016; MacLeod, 2009). An inability to shift their distribution, for example due to habitat preferences or physical barriers, might also genetically isolate certain cetacean populations and, thereby, likely reduce their genetic diversity (van Weelden et al., 2021).

Additionally, seawater temperature has been suggested to directly affect the population structure, genetic differentiation, and population isolation of long-finned pilot whale (*Globicephala melas*) populations in the North Atlantic (Fullard et al., 2000). Temperature changes due to ocean warming might influence these patterns.

Impacts of ocean acidification

The world's oceans absorb approximately 30% of anthropogenic carbon (Sabine et al., 2004), which is causing ocean acidification (IPCC, 2021). This phenomenon will continue to increase in the 21st century, and changes in deep ocean acidification will be irreversible on centennial to millennial time scales (IPCC, 2021).

In the Mediterranean Sea, acidification is currently occurring at a geologically unprecedented rate, subjecting many marine organisms to an additional, and worsening, environmental stressor (MedECC, 2020, UNEP/MAP, 2017) with significant negative impacts projected for e.g., calcifying organisms and marine biodiversity (Balzan et al., 2021; Riebesell et al., 2000; UNEP/MAP & Plan Bleu, 2020; Feely et al., 2004; Kleypas et al., 1999). Moreover, acidification affects many planktonic species (with possible negative effects on fish populations) and threatens iconic and invaluable Mediterranean ecosystem-building species that create rich habitats (such as sea grass meadows, coralligenous reefs and vermetid snail reefs) for a wide variety of species (MedECC, 2020; Lacoue-Labarthe et al., 2016). There will be shifts in the phytoplankton community, with dominance of smaller species and a decrease in the biomass of the largest size group, as well as changes in the magnitude and timing of phytoplankton blooms, with associated changes in the seasonal distribution of zooplankton (Balzan et al., 2021; Moullec et al., 2019) and cascading effects on fluxes of energy and matter in food webs (ACCOBAMS, 2021). Impacts on metabolic function, growth and reproduction of fish and invertebrates are also predicted (e.g., Gambainani et al., 2009; Pörtner et al., 2007; Orr et al., 2005; Royal Society, 2005), as well as on their distributions and habitat suitability (Clarke et al., 2021; Deutsch et al., 2020; Deutsch et al., 2015). Cephalopods will likely be particularly sensitive (e.g., Gambaiani et al., 2009).

Ocean acidification, alongside ocean warming, may impact cetaceans by affecting the availability and distribution of their prey (Nunny & Simmonds, 2021; Lacoue-Labarthe et al., 2016; Pace et al., 2015). One example from the Mediterranean region is the long-finned pilot whale, whose distribution and population structure could be affected as some of their prey, e.g., squid, are sensitive to temperature and ocean acidification (Nunny & Simmonds, 2021; Verborgh et al., 2016).

Impacts of sea level rise, ocean deoxygenation, and changes in salinity, nutrient availability, ocean circulation and currents, and large-scale atmospheric and ocean modes

Climate change is altering a variety of additional oceanographic and atmospheric features with consequences for marine life across the food webs. We discuss here in particular the impacts of sea level rise, ocean deoxygenation, ocean stratification, changes in ocean circulation and currents, and alterations to large-scale atmospheric and ocean modes.

Global mean sea level has risen faster over the past century than over any preceding century in at least the last 3,000 years, with a 0.2 [0.15-0.25] m rise over the period 1901-2018 (IPCC, 2021). It is virtually certain that it will continue to rise over the 21st century and is committed to rise for centuries to millennia due to continuing deep ocean warming and ice sheet melt (IPCC, 2021). It would take several centuries to millennia for global mean sea level to reverse course even under large net negative CO_2 emissions (IPCC, 2021). At a basin scale, sea level rose fastest in the Western Pacific and slowest in Eastern Pacific over the period 1993-2018 (IPCC, 2021).

Sea level rise, currently accelerating because of global ice loss (IPCC, 2021), threatens coastal ecosystems, enhances erosion and floodings (IPCC, 2021), and, in doing so, potentially increases agricultural (and other) runoff and thus nutrient input into the ocean, magnifying the exposure of coastal species to degradation and pollution (e.g., IPCC, 2022; Gossling et al., 2018; Enriquez et al., 2017; Geraci & Lounsbury, 2002).

Ocean deoxygenation – a decrease in the oxygen content of the upper ocean caused by ocean warming, stratification, and eutrophication – compounds on ocean warming and acidification. It will continue to increase in the 21st century and is irreversible on centennial to millennial timescales (IPCC, 2021). In its most extreme state, ocean deoxygenation can cause so-called "dead zones", regions with too little oxygen to sustain life. These areas are increasing and might continue to expand in the future (e.g., Wang et al., 2022; Stramma et al., 2008).

Decreasing oxygen levels due to warming are another threat to marine life and might be particularly problematic in enclosed areas such as the Black and Baltic Seas (Nunny & Simmonds, 2021; Reid, 2016).

The upper ocean has become more stably stratified since at least 1970 over the vast majority of the globe, primarily due to surface-intensified warming and high-latitude surface freshening (IPCC, 2021). Upper ocean stratification will continue to increase throughout the 21st century (IPCC, 2021). Such changes in ocean stability affect the vertical exchange of surface waters with the deep ocean and might affect large-scale ocean circulation (IPCC, 2021). By altering nutrient availability and mixing of gases, ocean stratification could also influence primary production and ocean productivity (e.g., Gacic, 2002; Roemmich & McGoan, 1995).

Global warming is also expected to alter ocean circulation and major ocean currents (IPCC, 2021). One example is the Atlantic Meridional Overturning Circulation (AMOC), which is projected to weaken over the 21st century (IPCC, 2021). While there is medium confidence that there will not be an abrupt collapse of the AMOC within this century, such a major climate tipping point cannot be ruled out completely (IPCC, 2021). Additionally, many ocean currents will change over the 21st century as a response to changes in wind stress associated with anthropogenic warming (IPCC, 2021).

Changes in water mass formation, mixing and upwelling patterns may affect marine biodiversity and ecosystems (IPCC, 2001a) and alter the distribution, abundance and migration of plankton, fish, and cephalopods (e.g., Planque & Taylor, 1998; Walther et al., 2002; Gambaiani et al., 2009) with subsequent effects on cetaceans (e.g., Bjorge, 2002).

In the Mediterranean Sea, increases in the frequency of large-scale atmospheric events (e.g., NAO, El Niño, SO, PDO) were found to affect the distribution, growth, abundance, and recruitment of marine organisms (Stenseth et al., 2002; IPCC, 2001a; Timmermann et al., 1999).

Cetaceans may be impacted by changes in prey availability caused by large-scale atmospheric events (Gambaiani et al., 2009), as well as altered prey distribution and abundance caused by changes in coastal water salinity and circulation patterns (e.g., Learmonth et al., 2006; MacGarvin & Simmonds, 1996). They might also experience (potentially lethal) poisoning due to increasing toxic algal blooms and higher exposure to pollutants (e.g., Häusserman et al., 2017; Learmonth et al., 2006; Burns, 2002; Geraci & Lounsbury, 2002; MacGarvin & Simmonds, 1996; Orr et al., 1992).

The largest reported mass mortality event in baleen (mainly sei, *Balaenoptera borealis*) whales in southern Chile in 2015 has been linked to a toxic algal bloom during a building El Niño event (Häusserman et al., 2017). The frequency of the strongest El Niño events is predicted to increase under climate change (Häusserman et al., 2017). Changes in ocean salinity can cause higher physiological stress, rendering cetaceans more susceptible to disease or anthropogenic pressures (Gambaiani et al., 2009; Learmonth et al., 2006; Wilson et al. 1999). Changes in current patterns might cause changes in migration routes and may also affect the transmission of sound and hence communication capacity (Gambaiani et al., 2009; IWC, 1997; Agardy, 1996; MacGarvin & Simmonds, 1996).

Impacts on reproductive success have been observed, for example, in Southern right whales (*Eubalaena australis*) in Brazil, where global climate indices such as the Oceanic Niño Index, the Antarctic Oscillation and Antarctic sea ice area indirectly affected breeding success by influencing krill availability (Seyboth et al., 2016).

Reduced reproductive success and habitat quality and shelter due to climate-driven increases in extreme weather events have been predicted for cetaceans that prefer calmer, reef protected waters for calving (e.g., Grose et al., 2020). In general, species that breed, feed, and calve in coastal areas are projected to be amongst those subjected to the strongest negative impacts from decreased habitat quality caused by global warming (Simmonds & Nunny, 2002; Agardy, 1996; Orr et al., 1992).

Range shifts in response to climate-driven changes in prey availability have been observed, for example, in North Atlantic right whales, that are now observed feeding in the Gulf of St. Lawrence – well north of their usual feeding grounds – in response to climate-driven changes in the Gulf Stream and, subsequently, warmer waters and less favourable feeding conditions in the Gulf of Maine and Scotian Shelf regions of the Northwest Atlantic (Meyer-Gutbrod et al., 2021; Meyer-Gutbrod et al., 2018). These alterations did not only diminish the whales' foraging opportunities and shift their late spring and summer distributions, but also impacted the whales' health and reproductive success (Meyer-Gutbrod et al., 2018; Meyer-Gutbrod & Greene, 2018; Pace et al., 2017; Rolland et al., 2016), increased the likelihood of ship strikes and entanglements (Meyer-Gutbrod et al., 2021; Daoust et al., 2017), and lengthened their migration routes to the breeding grounds off the South-eastern US coastline (Grose et al., 2020).

Additionally, changes in salinity have been linked to decreased health and impacts on cetaceans' immune systems (e.g., Gambaiani et al., 2009; Burek et al., 2008; Bearzi, 2002; Aguilar & Raga, 1993), as observed, for example, in a higher prevalence and severity of skin lesions in bottlenose dolphins (Learmonth et al., 2006).

Impacts of changes in sea ice

In the last decade, annual average Arctic sea ice area reached its lowest level since at least 1850, and late summer Arctic sea ice area was smaller than at any time in at least the past 1000 years (IPCC, 2021). The Arctic Ocean will likely become practically ice-free during the seasonal ice minimum for the first time before 2050 in all SSP scenarios, a state that might become the new normal by 2100 under continued high greenhouse gas emissions (IPCC, 2021). This might have major impacts on species at different levels of the trophic web that depend on sea ice for their survival, feeding, or reproduction.

Observed and projected impacts on cetaceans include effects on community structure (e.g., George et al., 2017; Heide-Jorgensen et al., 2012), habitat and distributional ranges (e.g., van Weelden et al., 2021; Brower et al., 2018, Storrie et al., 2018; George et al., 2017; Tsujii et al., 2016; Kaschner et al., 2011, MacLeod, 2009; Laidre et al., 2006; Heide-Jorgensen & Leidre, 2004), phenology and migrations (e.g., Brower et al., 2018; Hauser et al., 2017; O'Corry-Crowe et al., 2016; Tynan & Russel, 2008), reproductive output (Gulland et al., 2022; Perryman et al., 2021 & 2002), and health and survival (e.g., Raverty et al., 2020; Gulland et al., 2005; Le Boeuf et al., 2000).

Combined climate change impacts

Certain impacts on marine life arise from the cumulative effects of climate-induced changes to the oceans' physical or bio-chemical properties rather than any single mechanism. Such cumulative effects are, for example, projected to have the potentially to alter primary production and phytoplankton assemblages, which might lead to changes in the transfer to energy across trophic levels and, possibly, cause dramatic modifications to food web dynamics (ACCOBAMS, 2021; Moullec et al., 2016). Climate-induced stressors might also cause declines in *Posidonia* sea grass meadows with potential impacts on fish nurseries and water purification (Bombace, 2001; Francour, 1997; Orr et al., 1992). Fish are predicted to have smaller body sizes, smaller size at first maturity, and possible higher mortality rates due to climate change (Sumaila et al., 2011). Other impacts of cumulative and/or interacting effects of climate change include increases in species' metabolic demands, their genetic diversity and resilience, losses in suitable habitats, and decreased marine biodiversity and ecosystem resilience (e.g., ACCOBAMS, 2021; van Weelden et al., 2021; Albouy et al., 2020; Grose et al., 2020; Pinsky et al., 2020; Bryndum-Buchholz et al., 2019; IPCC, 2019; Gambaiani et al., 2009).

In the Mediterranean region, decreasing precipitation and intensifying and more erratic heavy rainfalls (UNEP/MAP & Plan Bleu, 2020) are expected to lead to longer dry periods, interrupted by extreme intense precipitation, which enhances the risk of floods (MedECC, 2020) and erosion, and likely impacts marine ecosystems (IPCC, 2022). Additionally, increases in the frequency of winter convection and subsequently increased phytoplankton biomass have been observed to lead to changes in the nutrient availability in surface waters of the Ligurian Sea, which is suspected might have cascading effects on Mediterranean biotic components from plankton to cetaceans (ACCOBAMS, 2021).

In various regions, recovery times for both marine environments and the megafauna that depends on them is expected to decrease as the predicted escalating intensity and, likely, frequency of storms (Bindoff et al., 2019) increase the magnitude of habitat destruction over succesive events (Grose et al., 2020; Thomas et al., 2016).

Range shifts or increased extinction risks are expected as climate change alters opportunities for shelter, reproduction, survival, and food (Grose et al., 2020), reduces fitness of individuals and populations, and possibly alters migration routes (e.g., Gambaiani et al., 2009; MacGarvin & Simmonds, 1996). Species whose movements are restricted by barriers, those that will not be able to shift to alternative food sources or broaden their diet, as well as coastal species are expected to be most vulnerable to these changes (Grose et al., 2020; MacLeod, 2009; Learmonth et al., 2006; Simmonds & Isaac, 2007; Simmonds & Nunny, 2002).

Climate-induced shifts in cetacean distribution might cause ecosystem-wide impacts as the cetaceans' ecosystem engineering services, including their roles in nutrient cycling and as predators feeding on most trophic levels, shift with them and might cause major alterations to community structure and ecosystem functioning (e.g., ACCOBAMS, 2021; van Weelden et al., 2021; Sadykova et al., 2020; Surma et al., 2014; Casini et al., 2012; Stachowicz et al., 2007; Dill et al., 2003).

Another example of ecological alterations caused by climate-induced range shifts of cetaceans may be a potential fiercer competition for euphausiids and copepods between Arctic and originally considered subarctic species, such as humpback and fin whales, in Arctic environments (Brower et al., 2018, Moore & Huntington, 2008).

A study modelling the impacts of different future climate scenarios on North Atlantic cetaceans' distributions found that striped dolphins might expand their ranges, while the suitable habitat of minke whales, white-beaked dolphins and Cuvier's beaked whales decreased – including a potential loss of up to 80% of suitable habitat for white-beaked dolphins (Lambert et al., 2014). Severe reductions in suitable habitat by 2100 have also predicted, for example, for Antarctic minke whales (Ainley et al., 2012; Tynan & Russel, 2008). Modelling of ocean warming and a resulting shift in the Antarctic circumpolar current also projected a southward shift and contraction of humpback, fin, blue and sperm whale feeding habitats in the Southern Ocean following an alteration in the availablity and distribution of their prey (Tynan & Russel, 2008).

Combined climate change effects might also lead to changes in migration routes (e.g., Gambaiani et al., 2005; MacGarvin & Simmonds, 1996) and changed cetacean presence in feeding and/or breeding grounds – an example of which are blue whales in the Northeast Pacific, which changed their presence at their feeding gounds in response to El Niño conditions, ocean warming, and a decline in seasonal upwelling that resulted in changes in the peak presence of their prey (Burtenshaw et al., 2004).

Cumulative effects of climate change and other stressors

When ecosystems are threatened by multiple, co-occurring drivers, climate change, environmental pollution (including plastic, noise, and chemical pollution), land and sea use change, invasive species, overexploitation, and other anthropogenic pressures can interact (IPCC, 2022). Such interactions cause effects that can be additive/cumulative, synergistic, or antagonistic and result in alteration, intensification, and even in generation of new impacts (IPCC, 2022).

In the Mediterranean region, climate change is already exacerbating pre-existing challenges, and combines with multiple human-induced pressures to impact already strained ecosystems, as well as biodiversity and ecosystem services (UNEP/MAP & Plan Bleu, 2020). These pre-existing pressures include pollution (including ocean noise, plastic pollution, emerging contaminants, and eutrophication), overfishing and unsustainable fishing practices, habitat degradation, invasive species, maritime transport, oil and gas exploration and exploitation, maritime spatial planning, and resource extraction as well as overexploitation thereof.

In the Mediterranean Sea, which is highly impacted by alterations to its food webs by overfishing, ocean warming is likely to further favour the dispersal and growth of 'jellyfish', which can control planktonic communities through predation of copepod and fish larvae (Balzan et al., 2021; Guerrero et al., 2018; Lejeusne et al., 2010). This is expected to alter the base of the food web, with possible cascading consequences for higher trophic levels (Balzan et al., 2021; Guerrero et al., 2018; Lejeusne et al., 2010).

One example in which the depletion of the main prey species driven by overfishing and eutrophication – which is predicted to increase under global warming – had drastic consequences on cetaceans are two mass mortality events of common dolphins in the Black Sea (Gambaiani et al., 2009; Birkun, 2002; Krivokhizhin & Birkun, 1999; Zaitsey & Mamaev, 1997).

An unexpected example of harmful interactions between extreme events and fisheries was found when humpback whales followed the inshore shift of forage fish caused by the unprecedented marine heatwave in the California Current ecosystem in 2014-2016. This shift coincided with the delayed Dungeness crab fishery and led to a dramatic spike in humpback whale entanglements (Ingman et al., 2021; Samhouri et al., 2021; Santora et al., 2020; Di Lorenzo & Mantua, 2016).

Conclusion

The wide variety of predicted and observed interactions between climate change and cetaceans is detailed above and outlined in Figure 1. The relevant literature is growing at an accelerating rate and, for the most part, the nature of the impacts on cetaceans, their prey and their habitats are of growing concern. Since the IWC last considered this matter in detail, at a virtual workshop in 2021, the IPCC (2022) has warned again that climate change is increasingly affecting marine ecosystems, that threats to species and ecosystems in the oceans, particularly in biodiversity hotspots, present a global risk that will increase with every additional degree of warming, and has reiterated its strong warning that effective action on climate change, whilst still feasible, needs to be actioned urgently.
The 2021 workshop made a series of recommendations for future action to both better understand and mitigate the effects of climate change on cetaceans (IWC, 2021). Its recommendations included that research was needed to 'inform a switch in the focus for management of cetaceans from sustainability to one of building resilience in their populations' and 'to identify priorities, including: high impact stressors, regions under the greatest threat, vulnerability windows and at-risk populations or species.' Further guidance for key actions is detailed in the workshop report.

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