



REVIEW

Global climate change, range changes and potential implications for the conservation of marine cetaceans: a review and synthesis

Colin D. MacLeod*

Institute of Biological and Environmental Studies (IBES), University of Aberdeen, Tillydrone Avenue, Aberdeen, AB24 3JG, UK

ABSTRACT: Global climate change has already resulted in an increase in oceanic water temperatures in some areas and is predicted to lead to further increases throughout much of the world in the foreseeable future. One possible response of cetacean species to these increases in water temperature is that species' ranges may change. Here, I provide a framework for assessing which cetacean species' ranges are likely to change as a result of increases in water temperature and whether they will expand, shift poleward or contract based on their current distributions. Based on this framework, it is predicted that the ranges of 88 % of cetaceans may be affected by changes in water temperature resulting from global climate change. For 47 % of species, these changes are anticipated to have unfavourable implications for their conservation, and for 21 % the changes may put at least one geographically isolated population of the species at high risk of extinction. This framework suggests that certain characteristics put some species at greater risk from such changes than others. These include a range that is restricted to non-tropical waters (including temperate species) and a preference for shelf waters. These characteristics are shared by most porpoises and *Lagenorhynchus* species and by all members of the genus *Cephalorhynchus*. As a result, species in these taxa are potentially at particular risk from changes in range in response to increasing water temperatures. However, further research is required to assess whether these predictions are, indeed, correct.

KEY WORDS: Global climate change · Cetaceans · Species ranges · Niche conservatism · Range changes · Conservation

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

The distributions of most species are defined by interactions between available environmental conditions and the ecological niches that they occupy. For marine cetaceans (hereafter cetaceans), ecological niches seem to be primarily defined by 3 factors. These are water temperature, water depth, and factors that affect the distribution and abundance of their prey (such as seabed topography, ocean currents and primary productivity), although other factors, such as predator avoidance and reproductive requirements, may also influence the distribution of some species to a lesser extent. Of these factors, the main influence on

geographic ranges of cetacean species appears to be water temperature, with the other factors primarily influencing how individuals are distributed within their ranges. Understanding the niche that a species occupies is important for species conservation. In particular, many organisms are thought to react to changes in their environment by changing their distribution to stay within the environmental envelope represented by their ecological niche (known as niche conservatism; Wiens & Graham 2005). Over time, niche conservatism means that the geographic range of a species may change as local, regional and/or global conditions change (Thomas et al. 2004, Wiens & Graham 2005). Such range changes are thought to be

*Email: c.d.macleod@abdn.ac.uk

one of the main mechanisms through which global climate change (GCC) is affecting, and will continue to affect, many animals and plants (Hughes 2000, Walther et al. 2002, Parmesan & Yohe 2003, Thomas et al. 2004, Wiens & Graham 2005), including marine species (e.g. Beaugrand et al. 2002, Perry et al. 2005, MacLeod et al. 2005).

In terms of cetaceans, it is widely accepted that geographic ranges of species restricted to polar zones, such as the narwhal *Monodon monoceros*, the beluga *Delphinapterus leucas* and the bowhead whale *Balaena mysticetus*, will be greatly affected by GCC. In particular, their ranges are expected to become greatly reduced as sea-ice coverage contracts and their distribution tracks the occurrence of this shrinking habitat (Tynan & DeMaster 1997, Harwood 2001, Simmonds & Isaac 2007). However, much less consideration has been given to the potential effects on temperate and tropical species. This is despite the fact that these species make up the majority of cetacean species, many of which are considered Vulnerable, Endangered or Data Deficient by the IUCN (Reeves et al. 2003).

Cetacean species' ranges and climate

While some cetacean species occur throughout the world's oceans (e.g. the killer whale *Orcinus orca* and the humpback whale *Megaptera novaeangliae*), the ranges of most cetacean species are geographically limited (Rice 1998). While these ranges may be the result of a number of factors, such as habitat preferences, evolutionary history of specific lineages and competitive interactions between species, the geographic ranges of many cetacean species are related to specific ranges of water temperatures (Kaschner et al. 2006). For example, white-beaked dolphins *Lagenorhynchus albirostris* are endemic to cooler waters of the northern North Atlantic (Rice 1998, Reeves et al. 1999), while the clymene dolphin *Stenella clymene* is limited to warmer sub-tropical and tropical waters of the Atlantic (Perrin & Mead 1995, Rice 1998). Yet, little research has been done on the exact climatic envelopes that define the niches occupied by individual cetacean species.

Similarly, it is currently unclear why cetacean species ranges are so often related to water temperature. Three possibilities have been hypothesized: (1) a species' range is a result of a direct relationship between water temperature and its thermal limits, although this seems unlikely given the fact that cetaceans are relatively large, well-insulated mammals (Watts et al. 1993, Learmonth et al. 2006); (2) a species' range is determined by the distribution of their preferred prey which are, in turn, directly affected by temperature (Learmonth et al.

2006, Simmonds & Isaac 2007); and (3) a species' range is determined by competitive interactions between ecologically similar species and the outcome of competition varies with water temperature (MacLeod et al. 2008). Further investigation is required to assess which, if any, of these hypotheses are correct.

How will cetacean species react to changes in water temperature?

GCC is anticipated to lead to a variety of changes to local environments. In particular, water temperatures have already increased due to the effects of GCC and are predicted to continue increasing throughout much of the world's oceans (Levitus et al. 2000, Barnett et al. 2001, Learmonth et al. 2006). Depending on the climate change scenario used, global surface temperatures are predicted to increase by between 1.1 and 6.4°C by the end of the 21st century (IPCC 2007). Where water temperatures increase, the current tropical zones are expected to expand into higher latitudes, temperate zones to shift polewards and polar zones to contract. In most cases, where a cetacean species' occurrence is restricted to specific temperature ranges, its geographic range would be expected to change to remain within the preferred climatic conditions (Thomas et al. 2004, Wiens & Graham 2005).

With a detailed knowledge of the climatic preferences and other aspects of the ecology of individual species it may be possible to produce detailed predictions of how individual species will react to GCC (e.g. Thomas et al. 2004, Araújo et al. 2005, but see Davis et al. 1998 for potential problems with this approach, such as their failure, in some cases, to consider non-climatic factors affecting species distribution). However, while it appears that the ranges of many cetacean species are limited to specific climatic conditions (Rice 1998, Kaschner et al. 2006), based on currently available information, it is not usually clear why this is the case or what the exact temperature limits of many cetacean species are. This causes a problem when trying to assess or predict exactly how the ranges of cetacean species are likely to change in response to GCC. In particular, it limits the current ability to provide quantitative assessments of how and when species ranges will change.

However, even if the exact extent of any changes may be hard to predict with the currently available information, given the fact that changes in water temperature and apparent impacts on marine organisms, including cetaceans, are already being detected (e.g. Beaugrand et al. 2002, Perry et al. 2005, MacLeod et al. 2005), it is important to understand which, if any, cetacean species ranges may change in response to

GCC. In particular, it is important to know if there is likely to be a decline in the total geographic area where a species occurs as the range changes in response to GCC. This is because there is a general ecological relationship between range size and population size (Lawton 1993, Gaston et al. 1997, Gaston & Curnutt 1998, Thomas et al. 2004) that has important implications for species conservation (Lawton 1993, Thomas et al. 2004). Species with smaller ranges, and therefore smaller population sizes, generally have a greater risk of extinction (Thomas et al. 2004).

Here, I provide a qualitative framework for understanding the likely direction of changes in cetacean species ranges resulting from GCC given the currently available information. Specifically, I propose that cetaceans can be divided into 4 basic climatic groupings based on their current ranges. Within these groupings, geographic ranges are anticipated to change in a qualitatively similar direction. However, the exact form and extent of the response of individual species within these general patterns may be modified by a variety of other factors. In particular, they may be modified by barriers that prevent a species colonising otherwise suitable habitat or tracking preferred temperature ranges (Simmonds & Isaac 2007; see 'Materials and methods: Barriers to tracking preferred temperature ranges'). Therefore, these aspects of cetacean species range are also considered. Through these considerations, I build up a number of hypotheses regarding which characteristics may make a cetacean species more likely to be negatively affected by GCC in terms of its geographic range.

MATERIALS AND METHODS

Cetacean species climatic groupings and their likely response to changes in water temperature.

Cetacean species were first classified into 4 categories based on how their ranges are likely to change in response to changes in water temperature rather than on their actual temperature preferences. This provides the advantage that species can be classified into a smaller number of categories and that these categories have a direct connection to the potential conservation implications of such changes. These categories were:

Cosmopolitan species: These are species that currently occur in all water temperatures from ice-edge to tropical waters, though the density of individuals within this range may vary with water temperature (e.g. killer whales; Dahlheim & Heyning 1999), sexual segregation (e.g. sperm whales *Physeter macrocephalus*; Rice 1989, 1998) or seasonal migrations (e.g. humpback whales; Winn & Reichley 1985, Rice 1998). Due to their cosmopolitan distribution it is unlikely that

the ranges of these species will be substantially altered as a result of climate change.

Cooler water-limited (CWL) species: CWL species occur from the ice-edges of polar waters to waters of a specific temperature range (see Fig. 1A for a theoretical example). As a result, it is likely that the ranges of these species are restricted only by warmer water temperatures at lower latitudes. The exact upper water temperature limit varies from species that are restricted to polar waters (e.g. the narwhal; Hay & Mansfield 1989) to species that also occur in temperate waters (e.g. the northern bottlenose whale *Hyperoodon ampullatus*; Mead 1989); however, the ranges of these species are predicted to consistently contract polewards in response to increasing water temperatures, resulting in a reduction in the area occupied (see Fig. 1B for a theoretical example).

Cooler and warmer water-limited (CWWL) species: CWWL species are typified by a range that is limited to waters of intermediate temperature and that do not cross the equator at any point or extend into cooler waters closer to the poles (see Fig. 1C for a theoretical example). As a result, these species are likely to have both an upper and a lower temperature limit to their species' ranges. Under GCC, while the poleward side of their ranges may expand into areas that were previously too cool, it is anticipated that this will be accompanied by a concordant contraction in their ranges from waters that have become too warm. This means that CWWL species' ranges are unlikely to increase; rather their ranges will shift polewards as water temperatures warm (see Fig. 1D for a theoretical example). The exact extent of this geographic shift will depend on how water temperatures change and the exact upper and lower water temperature limits of the species involved. Due to the spheroid nature of the Earth (and the fact that temperature is to a greater or lesser extent linked to latitude), such a poleward shift in distribution is likely to result in a decrease in the total area of the species range.

Warmer water-limited (WWL) species: WWL species are defined as those species with a continuous cross-equatorial range in at least one ocean that do not also occur in cooler waters of the same ocean(s) (see Fig. 1E for a theoretical example). These species are united by the fact that their ranges are probably only restricted by their ability to occur in cooler waters at the higher latitude edges of their ranges. Different species in this category may have very different lower temperature limits to their species' range (Appendix 1, Table A1). However, WWL species, regardless of the exact lower temperature limit to their range, are expected, where possible, to expand their geographic ranges polewards into areas where the water temperatures were previously too cool, increasing the geographic area occupied by such species (see Fig. 1F for a theoretical example).

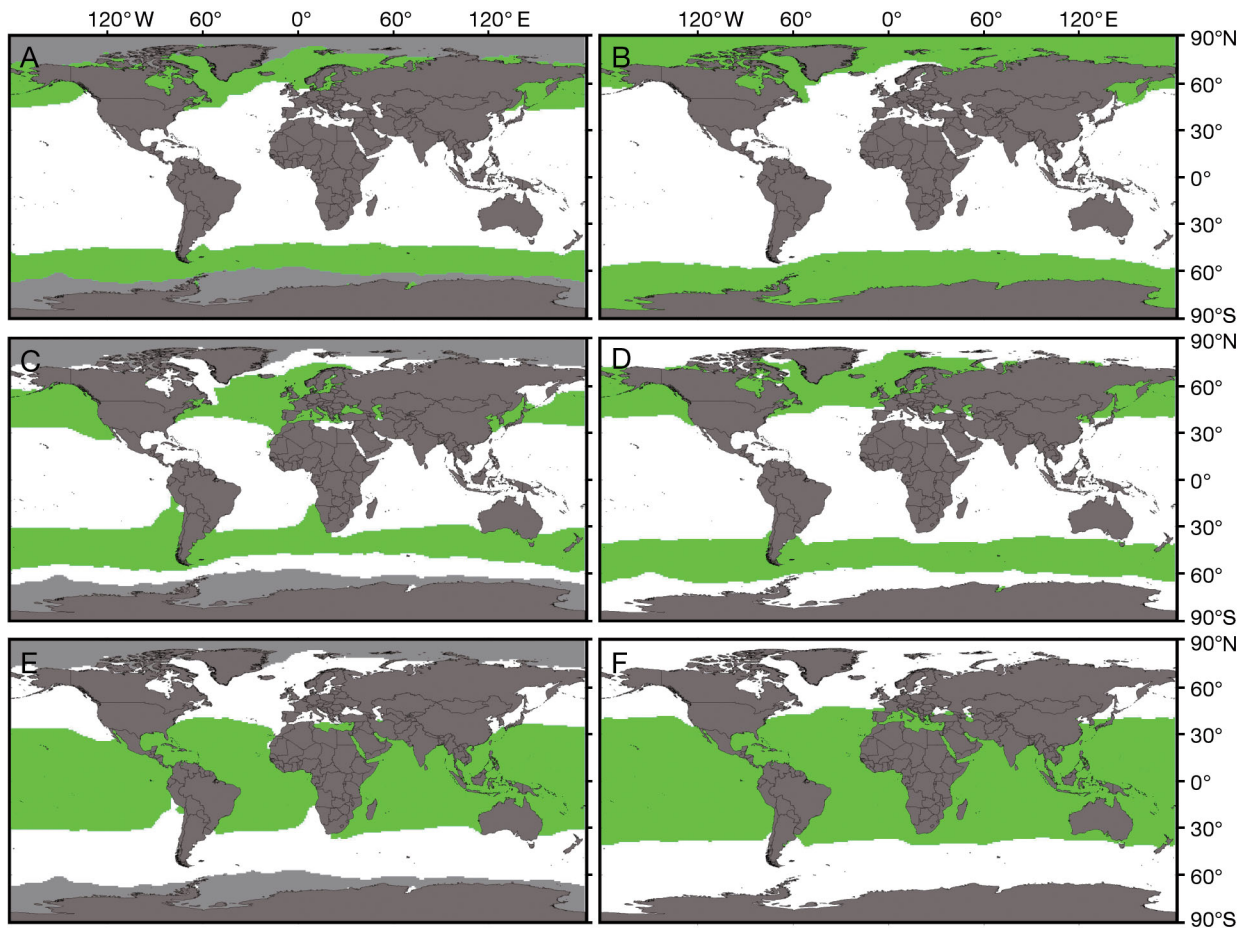


Fig. 1. Theoretical examples and directions of change in species' range in response to increases in water temperature driven by global climate change for 4 climatic categories of cetaceans. Cooler water-limited (CWL) species: (A) theoretical example of current range; (B) expected contraction in species range. Cooler and warmer water-limited (CWWL) species: (C) theoretical example of current range; (D) expected poleward shift in species range. Warmer water-limited (WWL) species: (E) theoretical example of current range; (F) expected expansion of species range. In all cases, a 5°C increase in temperature was used to illustrate the direction of change using temperature data from the World Oceans Atlas 2001 (www.nodc.noaa.gov/OC5/WOA01/pr_qoa01.html). However, while the actual extent of warming may vary, the direction of change would be expected to be the same for each category

Barriers to tracking preferred temperature ranges.

While species within each of these climatic groupings are, in theory, likely to respond in a similar direction to changes in water temperature, how individual species actually respond to such changes may be modified by the existence of barriers to species occurrence that are not associated with water temperature or other aspects of the oceanic climate. Specifically, in some cases, barriers may prevent a species from tracking its preferred water temperature range as it shifts in response to climate change. For example, the land mass of Asia may limit any potential poleward shift or expansion of cetacean species' ranges in the northern Indian Ocean.

Similarly, many species are restricted to specific water depth ranges. As a result, substantial discontinuities in waters of a specific depth range may prevent some species from tracking their preferred

temperature ranges as water temperatures increase in response to GCC. The potential for bathymetric discontinuities to modify the expected change in species' ranges was assessed by classifying each species based on whether its occurrence is restricted to shelf waters, to oceanic waters or whether it occurs in both (again unless otherwise stated, based on data from Rice 1989 and Kaschner et al. 2006). Information from the General Bathymetric Chart of the Oceans (GEBCO) Digital Atlas (IOC et al. 2003) was then used to identify the distribution of such waters within the current range of each species and in neighbouring waters into which its range is likely to shift. This then allowed any potential bathymetric barriers to be identified and used to modify the predicted change in species range and, therefore, in conservation status.

Potential releases on species' range. While the ability of some species to react to changes in water temperature resulting from GCC may be limited by the existence of barriers to alterations in their range, for other species existing barriers that prevent species colonising otherwise suitable temperature zones could be weakened, or even disappear completely, as water temperatures warm. For example, some cetacean species that are currently restricted to the warmer waters of the Atlantic Ocean may be prevented from colonising otherwise suitable warm water areas in the Pacific and Indian Oceans by the presence of cooler waters connecting these regions (e.g. around the Cape of Good Hope and Cape Horn; Fig. 2). Similarly, species currently restricted to cooler waters to the North Atlantic may be prevented from colonising the otherwise suitable North Pacific (and vice versa) by the presence of very cold water and sea ice in the Arctic Ocean and neighbouring sea areas, particularly in the northwest passage to the north of Canada, to the north of Greenland and to the north of Eurasia (Fig. 2). Climate change could potentially act as a releaser for such species allowing them to expand into these previously uncolonised (by the species in question), but otherwise apparently suitable, areas. For the present analysis, this was considered by examining whether there were any areas of apparently suitable habitat where an individual species does not currently occur and what barriers would need to be overcome for such areas to be colonised.

Potential conservation implications of changes in species range. Finally, given the climatic groupings outlined above and the potential, in the case of individual species, for modification of the predicted changes by the presence of barriers and releasers, the potential conservation implication of the predicted range change was assigned to 1 of 5 qualitative categories. These categories were primarily defined by the potential direction of change in the total geographic area

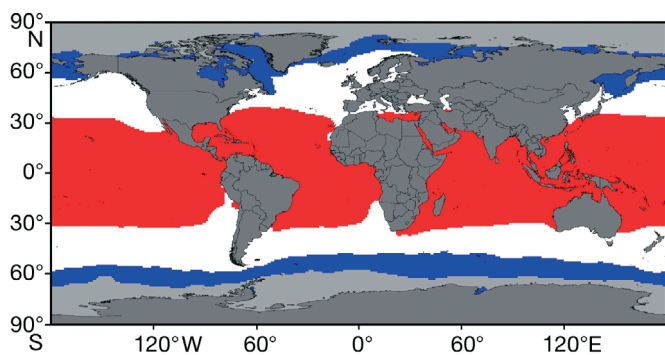


Fig. 2. Difference in extent of water temperature zones in different regions of the world's oceans. Light grey: sea ice; blue: sub-polar to polar waters (<5°C); white: temperate waters (5 to 20°C); red: subtropical to tropical waters (>20°C). Temperature data are long-term annual averages from the World Oceans Atlas 2001 (www.nodc.noaa.gov/OC5/WOA01/pr_woa01.html)

occupied by each species and assignment of species to categories was based on the general ecological principle that a smaller geographic range is likely to support a smaller population size and lead to an increased risk of extinction (Roberts & Hawkins 1999, Thomas et al. 2004). These were:

Favourable: The total geographic area of the species range is predicted to increase in response to increases in water temperature associated with GCC. An increase in geographic range may occur through a poleward expansion of the current range within the ocean areas a species currently occupies, or through the colonisation of a new ocean area.

Unchanged: The total geographic area of the species range is predicted to be unaffected by increases in water temperature.

Unfavourable: The total geographic area of the species range is predicted to decrease in response to increases in water temperature. A reduction in geographic range may occur either through a contraction in the current range or through a range shift into higher latitudes (due to the spheroid nature of the earth).

High risk: The total geographic area of the species' geographic range is predicted to decrease substantially in response to increases in water temperature and could contribute to a significantly increased risk of extinction of at least 1 geographically isolated population. This increased risk of extinction is primarily due to the entire current range of a geographically isolated population becoming unsuitable for it, with little option for habitat tracking due to the existence of barriers.

Unknown: There is insufficient information about the current geographic range and preferences for water temperature and depth to assess how range is likely to change in response to increases in water temperature.

In species with contiguous geographic ranges, a single assessment of the conservation implication was conducted. However, for species with populations separated by substantial barriers (e.g. shelf species in the eastern and western Atlantic, or tropical species in the Indian and Atlantic Oceans), each geographically isolated population was considered separately. Finally, it should be noted that these conservation implications are only intended to apply to range changes resulting from climate change and do not include a consideration of any other factors or the current conservation status of the species considered below.

RESULTS

While the exact relationship between the geographic limits of cetacean species' ranges and water temperature remains poorly known for most species, based on the framework developed here, the ranges

of the majority (88%) of cetacean species are predicted to change as a consequence of increases in water temperature resulting from GCC (Table 1, see Appendix 1 for a summary of individual species accounts and classifications). However, while the ranges of 50% of species are predicted to decline either due to a contraction or poleward shift, for 38% of species, range expansion is predicted (Table 1). For 47% of cetacean species, such range changes, if they were to occur, have the potential to have unfavourable implications for species conservation and in 21% of species the predicted range changes could put at least 1 geographically isolated population of a species at high risk of extinction (Table 2, see Supplement 1, available at www.int-res.com/articles/suppl/n007p125_app.pdf for full details).

Not all taxonomic groups of cetaceans are predicted to be affected to a similar extent (Tables 1 & 2). For example, while range changes are predicted to have no effect or a favourable effect on the conservation status

of 69% of baleen whales and all 3 sperm whale species, the conservation implications for both monodontids and 83% of porpoise species are expected to be negative. Similarly, within the dolphins, for most of the 'blackfish' (pilot whales *Globicephala* spp., false and pygmy killer whales *Psuedorca carassidens* and *Feresa attenuate*, respectively, and melon-headed whales *Peponocephala electra*) and all species in the genus *Stenella*, the changes are predicted to have no effect or a favourable effect on their conservation. In contrast, in the genera *Lagenorhynchus* and *Cephalorhynchus*, 60 and 100%, respectively, of species are could potentially have a high risk of extinction of at least 1 population if the predicted range changes were to occur.

These differences are due to specific characteristics that tend to typify these taxonomic groupings. For example, species which occur in tropical waters (e.g. *Stenella* species) are generally predicted to do better than species that are restricted to non-tropical (polar and/or temperate, e.g. *Lagenorhynchus* species) and polar waters (e.g. monodontid species). Similarly, species that occur at all water depths and those restricted to oceanic waters (e.g. *Stenella* species) are expected to do better than those restricted to shelf waters (e.g. *Cephalorhynchus* species) due to the greater extent of bathymetric barriers separating shelf areas.

Table 1. Summary by taxonomic groupings of predicted changes in marine cetacean species' ranges in response to increases in water temperature resulting from global climate change (Appendix 1; see also Supplement 1, available at www.int-res.com/articles/suppl/n007p125_app.pdf, for full details)

Cetacean family	Range expansion	Range shift	Range contraction	No change	Unknown	Total
Baleen whales	3	4	1	5	0	13
Beaked whales	6	8	5	0	2	21
Sperm whales	2	0	0	1	0	3
Marine river dolphins	0	1	0	0	0	1
Monodontids	0	0	2	0	0	2
Dolphins	18	6	7	1	0	33
Porpoises	1	1	4	0	0	6
Total	30	20	19	7	2	78

Table 2. Summary by taxonomic groupings of expected conservation implications of changes in marine cetacean species' ranges in response to increases in water temperature resulting from global climate change by. When different geographically isolated populations of a species have more than one conservation classification, the one with the greatest conservation implications is included in this summary (see Appendix 1 and Supplement 1 for full details)

Cetacean family	Favourable	Unchanged	Unfavourable	High risk	Unknown	Total
Baleen whales	3	6	2	2	0	13
Beaked whales	5	1	12	0	3	21
Sperm whales	2	1	0	0	0	3
Marine river dolphins	0	0	1	0	0	1
Monodontids	0	0	0	2	0	2
Dolphins	18	1	5	8	0	32
Porpoises	1	0	1	4	0	6
Total	29	9	21	16	3	78

DISCUSSION

The present qualitative study suggests that range changes resulting from changes in water temperature caused by GCC may potentially affect the majority of cetacean species. In many cases, these range changes are expected to have negative consequences for the conservation status of individual species, and in one case an entire genus. While this is not necessarily unexpected, by applying the framework outlined above, the present study has, for the first time, attempted to identify which characteristics may make some species more vulnerable than others to such changes. In particular, the present study suggests that it is not just polar cetacean species that are particularly vulnerable to the effects of GCC, and also highlights the importance of considering non-climatic elements when

assessing potential changes to species' ranges resulting from GCC. In particular, the results of the present study suggest that local bathymetry and a species' habitat preferences can potentially combine to trap a species or geographically isolated population within a specific geographic area, greatly limiting its ability to track its preferred temperature ranges as water temperatures increase, with resulting conservation implications.

Is there evidence that cetacean ranges respond to changes in temperature in the predicted manner?

While it is clear that the geographic ranges of many cetacean species are limited to specific water temperature ranges (Rice 1998, Kaschner et al. 2006), there is little direct evidence that these geographic ranges actually change in response to changes in water temperature in the predicted manner. However, rather than this necessarily being due to a lack of such a linkage between the two, it is possible, instead, that it is due to a lack of suitable data for detecting such changes, such as long time-series of species occurrence and concurrent measures of water temperature.

In the few cases where sufficient suitable data are available, species ranges and occurrence have been found to change in the predicted manner. For example, in the early 1990s, strandings of dolphin species in northwest Scotland were dominated by the white-beaked dolphin, a CWWL species close to the southern limit of its current range. However, by the early 2000s its occurrence had declined substantially and it had been replaced in the strandings record by 2 warmer water species whose ranges had expanded northwards as temperatures increased across this period (MacLeod et al. 2005). Similarly, since 1988, 3 warm water species were recorded in northwest Scotland for the first time, consistent with the predicted northward expansion of their species' ranges as temperatures increased (MacLeod et al. 2005). At the same time, there were declines in the occurrence of 4 cold water species (white-beaked dolphin, long-finned pilot whale *Globicephala melas*, northern bottlenose whale and Sowerby's beaked whale *Mesoplodon bidens*) consistent with a contraction in their species' ranges (MacLeod et al. 2005). Similar changes have also been detected in sightings data. For example, in the Bay of Biscay, sightings of the northern bottlenose whale, a cool water species, declined between the early 1990s and the late 2000s consistent with a contraction in the species' range as temperatures have increased in recent years, while sightings of the warmer water Cuvier's beaked whale *Ziphius cavirostris* have increased and spread northwards in this region (J. Smith pers. comm.). This suggests that changes in

the occurrence of cetacean species consistent with those predicted from the present study are already occurring in the northeast Atlantic in response to increases in water temperature. The species apparently affected so far have very different ecologies, suggesting that such changes are relatively widespread across the local cetacean assemblages and are not limited to any specific ecological type. In addition, studies of other marine organisms show similar trends within the same region (e.g. turtles, McMahon & Hays 2006; plankton, Beaugrand et al. 2002; fish, Perry et al. 2005), suggesting that cetaceans are no different in this respect than other organisms.

Geographic variations in changes in species' ranges

When considering how cetacean species ranges are likely to respond to increases in water temperature there is a potential for differences in the extent of the changes in ranges in different geographic areas. This is primarily due to 2 factors.

Firstly, the latitudinal gradients in water temperature are not identical throughout the world's oceans. For example, in the western North Atlantic, the distance between sub-tropical (indicated by the 20°C long-term average annual isotherm) and sub-polar (indicated by the 5°C long-term average annual isotherm) waters is only about 15 degrees of latitude, or approximately 1500 km in some places (Fig. 2). In contrast, in the eastern North Atlantic, the distance between the 20 and 5°C isotherms is more than 40 degrees of latitude (or >4000 km) spanning an area between the Canary Islands in the south and northern Norway in the north (Fig. 2). As a result, the same increase in water temperature in these 2 areas may result in very different changes in the geographic range of an individual cetacean species, with it being much greater in the eastern than the western Atlantic. Relatively large changes in the geographic range of individual cetacean species with relatively small changes in water temperature may also occur in areas such as the northeast Pacific, the southeast Pacific and the southeast Atlantic where the latitudinal gradient in temperatures (as indicated by the distance between the 5 and 20°C isotherms) is less steep (Fig. 2).

Secondly, there is likely to be geographic variation in the exact extent of the temperature change associated with GCC, meaning that cetacean communities and species with ranges restricted to certain parts of the world may be affected to a greater extent than those in others. In particular, changes in regional sea temperatures may be modified by changes in the strength and course of currents, upwellings and downwellings, and changes in regional climatic conditions such as wind

strength and storm frequencies. Therefore, these geographic variations also need to be taken into account when considering how future changes in climate will affect the extent of range changes for species within specific regions or areas.

Species' range expansion and colonisation of new ocean areas

The expansion of some species' geographic ranges as a response to increases in water temperature could, at least theoretically, lead to species colonising new areas. In particular, the land mass of southern Africa creates a barrier to the dispersal of certain species between the tropical and sub-tropical waters of the Indian and Atlantic Oceans. This is because the area of cooler water around the southwest tip of Africa (Fig. 2) is likely to be unsuitable habitat for such species. However, even a relatively small increase in water temperatures in this region, possibly as little as 2 to 4°C (well within the range predicted under some climate change scenarios; IPCC 2007), may result in the disappearance of this barrier for some species. This could, in turn, lead to the creation of novel communities of species with new interspecific interactions. A similar situation may exist in the eastern Mediterranean, which is isolated from waters of similar temperatures by the cooler waters of the eastern Atlantic around the Straits of Gibraltar (Fig. 2). Currently the eastern Mediterranean is relatively species-poor and lacks many of the tropical and sub-tropical species found in the Atlantic, including various *Stenella* species, warm-water *Mesoplodon* species, such as Gervais' beaked whale *Mesoplodon europaeus*, and a number of blackfish species. With sufficient warming of the eastern Atlantic and western Mediterranean around the Straits of Gibraltar, there is the potential for some or all of these species to colonise the otherwise suitable waters of the eastern Mediterranean.

The results of such interactions are extremely difficult to predict and may have many unforeseen consequences. For example, a new species may competitively exclude an existing species from some or all of its current range and/or preferred habitats. Similarly, the novel mixing of species, or indeed previously isolated populations of the same species, may result in the introduction of novel pathogens and/or parasites into naive populations with potentially serious consequences. Finally, the mixing of previously isolated populations of the same species may result in a loss of genetic uniqueness of these populations. One of the most interesting examples of this type of potential interaction is the case of the 2 humpback dolphin species. The Atlantic and Indian Ocean members of the genus *Sousa* are currently considered separate, but

allopatric, sister species. Considering that interspecific hybridisation is not uncommon between cetacean species, even of different genera (e.g. Reyes 1996, Zornetzer & Duffield 2003, Willis et al. 2004), it is likely that the 2 species would be able to interbreed if they were to occur in sympatry. With sufficient overlap in the species ranges and high levels of interbreeding, this may lead to a loss of the genetic separation between these 2 species and the collapse of the current allospecies into a single genetic entity. The conservation implications of such an event are unclear as it could either be considered a natural event within a lineage or as a loss of genetic uniqueness of isolated populations.

Migratory species, GCC and cetacean species' range

The present study has primarily concentrated on the effects of GCC on geographic ranges as a whole. However, in a small proportion of cetacean species (primarily the baleen whales and the sperm whale) there are discrete migratory movements within their geographic range, which means that some sections are only occupied during part of the year or specific periods of their breeding cycle. As these sections are occupied for different reasons, this may mean that GCC has different effects on different parts of the geographic range. For example, in the eastern Pacific, the grey whale migrates between feeding areas in sub-polar to temperate regions in the north and calving/breeding areas in subtropical coastal lagoons in the south. If GCC has a different effect on the feeding and breeding areas, this could result in changes in the length and/or timing of migrations between these regions. However, we currently know very little about why these migratory movements evolved and why specific areas are chosen for calving and breeding that are so distant from the areas used for feeding. As a result, it is difficult to predict how GCC may affect the suitability of these areas, and therefore how GCC may affect migratory movements within a species' given geographic range.

Potential implications for other conservation issues

Range changes resulting from changes in water temperature will not occur in isolation, but instead will interact with other threats to cetacean species such as bycatch, habitat degradation, overfishing of prey species and pollution. However, the conservation measures for almost all other threats require that we understand not only the current range of a species or population, but also whether and how this range is likely to change in the future. If such changes can be predicted in advance, conservation measures can be

amended proactively before they start to become less effective, rather than reactively after the changes have occurred. Therefore, any factors which may affect the range of cetacean species represent a fundamental issue for future cetacean conservation.

Similarly, it is probable that the conservation implications of range changes resulting from GCC proposed here will be modified by other factors, including other potential impacts of climate change. However, they provide a useful indication of those species which may be particularly vulnerable to the effects of changes in their ranges in response to increasing water temperatures (which has the potential to be one of the most widespread effects of climate change on cetacean species) and, when combined with information about other known or potential threats, this will increase our ability to conserve cetaceans that are under threat.

In addition, changes in the ranges of cetaceans will not occur in isolation and will be only one of many types of change at all levels of marine ecosystems. In particular, cetaceans represent only one component of an ecosystem within a biogeographic zone, whereas all components may be affected by changes in water temperature. However, cetacean occurrence can be assessed and monitored with relative ease in comparison to many other marine organisms. Therefore, there is the potential for cetaceans to be used as indicators of range changes in other marine organisms or marine ecosystems as a whole (see Newson et al. 2009 for details of what makes a good indicator for this purpose). However, further research is required to establish the exact nature of such linkages between cetaceans and other marine organisms in order to establish the effectiveness of using some or all cetacean species as indicators of range changes in other marine organisms.

What characteristics make a cetacean species vulnerable to potentially negative impacts of range changes resulting from GCC?

In the course of the present study, several characteristics seemed to be consistently associated with unfavourable or high risk classifications for the implications on conservation status. As a result, I propose the following hypotheses regarding which characteristics make some cetacean species more vulnerable to negative impacts of range changes resulting from GCC than others:

(1) CWL or CWWL species: The ranges of these species are expected to contract or shift polewards, resulting in a decrease in the geographic size of the species range. These categories include many temperate as well as polar and sub-polar species.

(2) Species for which land barriers or discontinuities in preferred seabed bathymetry will prevent range shifts in response to changes in water temperature. This is particularly an issue for species limited to shelf waters as such waters tend to have the greatest discontinuities around the world.

(3) Species or populations which occur in areas with a shallow latitudinal temperature gradient within, at or close to the edges of the current species' temperature range. As a result, even a small change in water temperature in an unsuitable direction may have a large effect on the geographic range of the species or population involved.

(4) Species which are adversely affected by the colonisation of their range areas by additional species due to the disappearance of existing barriers between otherwise suitable ocean areas. This potential impact will be the hardest to predict in advance as determining the outcome of competitive interactions between previously non-interacting species may be particularly challenging.

At least 3 of these proposed characteristics are shared by most porpoise and *Lagenorhynchus* species, and by all members of the genus *Cephalorhynchus*, and in combination are responsible for the high percentages of species in these genera predicted to be negatively affected by range changes resulting from climate change. Similar factors, amongst others, have previously been linked to extirpation and extinction risks in marine species in general (Roberts & Hawkins 1999).

Future research

Given the potential for GCC to affect cetacean conservation status, the present study highlights the need for further research in a number of currently poorly known areas of cetacean ecology if we are to understand why and how cetacean species' ranges may be affected by GCC. Firstly, there is a need to assess whether and how individual cetacean species' ranges are, indeed, related to water temperature. Secondly, there is a need to investigate whether the ranges of species that are apparently limited to specific temperature ranges are, in fact, driven by water temperature rather than by other factors which currently covary with temperature. Such research can be achieved using data from traditional surveys (e.g. MacLeod et al. 2008) or more recent satellite telemetry and remote sensing information (e.g. McMahan & Hays 2006) to correlate cetacean occurrence and sea temperature. While this may seem like a basic issue, it has yet to be properly resolved for most cetacean species. Only once this has been achieved can we assess the likelihood of the potential changes in cetacean range outlined here

actually occurring. When this has been clarified, there is a need to assess whether these relationships are direct, e.g. due to the limits of a species thermal neutral zone, or whether they are indirect, e.g. due to an effect on preferred prey species. This is important to understand as it will clarify how the basic assessments outlined in the present study need to be modified to better reflect the potentially complex interactions between cetacean ranges and water temperature. Again, little such research has been conducted to date in this area. There is also a great need for research assessing whether and how species ranges do in fact alter in relations to changes in water temperature. While the work outlined above does suggest this is the case, the evidence to date primarily comes from a single region, the northeast Atlantic. As a result, it is important to assess how representative this area is of other parts of the world, and indeed how representative the species examined to date are of cetaceans as a whole. Finally, once our understanding of how cetacean species ranges are related to water temperature has increased, it is important that the results are applied to various future scenarios of likely changes in water temperature.

Acknowledgements. This study was developed, in part, from work carried out at the University of Aberdeen on 2 projects, funded by the Department for Environment, Food and Rural Affairs (DEFRA) and coordinated by the British Trust for Ornithology (BTO), which examined the effects of climate change on migratory species (Climate Change and Migratory Species Report for DEFRA Research Contract CR0302 and Indicators of the Impact of Climate Change on Migratory Species Report for DEFRA Research Contract CR0363). The author thanks S. Bannon, J. Learmonth, S. Mendes, G. J. Pierce, K. Hall and the 3 anonymous referees for their comments and suggestions on various drafts of this manuscript.

LITERATURE CITED

- Araújo MB, Whittaker RJ, Ladle RJ, Erhard M (2005) Reducing uncertainty in projections of extinction risk from climate change. *Glob Ecol Biogeogr* 14:529–538
- Barnett TP, Pierce DW, Schnur R (2001) Detection of anthropogenic climate change in the world's oceans. *Science* 292:270–274
- Beaugrand G, Reid PC, Ibañez F, Lindley JA, Edwards M (2002) Reorganization of North Atlantic marine copepod biodiversity and climate. *Science* 296:1692–1694
- Dahlheim ME, Heyning JE (1999) Killer whale: *Orcinus orca* (Linnaeus, 1758). In: Ridgway SH, Harrison RJ (eds) *Handbook of marine mammals, Vol 6: the second book of dolphins and the porpoises*. Academic Press, Cambridge, p 281–322
- Davis AJ, Jenkinson LS, Lawton JL, Sharrocks B, Wood B (1998) Making mistakes when predicting shifts in species range in response to global warming. *Nature* 391:783–786
- Gaston KJ, Curnutt JL (1998) The dynamics of abundance–range size relationships. *Oikos* 81:38–44
- Gaston KJ, Blackburn TM, Lawton JH (1997) Interspecific abundance–range size relationships: an appraisal of mechanisms. *J Anim Ecol* 66:579–601
- Harwood J (2001) Marine mammals and their environment in the twenty-first century. *J Mammal* 82:630–640
- Hay KA, Mansfield AW (1989) Narwhal: *Monodon monoceros*, Linnaeus, 1758. In: Ridgway SH, Harrison RJ (eds) *Handbook of marine mammals, Vol 4*. Academic Press, London, p 145–176
- Hughes L (2000) Biological consequences of global warming: Is the signal already apparent? *Trends Ecol Evol* 15:56–61
- IOC, IHO, BODC (2003) Centenary Edition of the GEBCO Digital Atlas. Intergovernmental Oceanographic Commission and the International Hydrographic Organization, General Bathymetric Chart of the Oceans, British Oceanographic Data Centre, Liverpool
- IPCC (2007) *Climate Change 2007: synthesis report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. IPCC, Geneva, www.ipcc.ch/pdf/assessment-report/ar4/syr/ar4_syr.pdf
- Kaschner K, Watson R, Trites AW, Pauly D (2006) Mapping worldwide distributions of marine mammal species using a relative environmental suitability (RES) model. *Mar Ecol Prog Ser* 316:285–310
- Lawton JH (1993) Range, population abundance and conservation. *Trends Ecol Evol* 8:409–413
- Learmonth JA, MacLeod CD, Santos MB, Pierce GJ, Crick HQP, Robinson RA (2006) Potential effects of climate change on marine mammals. *Oceanogr Mar Biol Annu Rev* 44:431–464
- Levitus S, Antonov JI, Boyer TP, Stephens C (2000) Warming of the world ocean. *Science* 287:2225–2229
- MacLeod CD, Bannon SM, Pierce GJ, Schweder C, Learmonth JA, Reid RJ, Herman JS (2005) Climate change and the cetacean community of northwest Scotland. *Biol Conserv* 124:477–483
- MacLeod CD, Weir CR, Santos MB, Dunn TE (2008) Temperature-based summer habitat partitioning between white-beaked and common dolphins around the United Kingdom and Republic of Ireland. *J Mar Biol Assoc UK* 88:1193–1198
- McMahon CR, Hays GC (2006) Thermal niche, large scale movements and implications of climate change for a critically endangered marine vertebrate. *Glob Change Biol* 12:1330–1338
- Mead JG (1989) Bottlenose whales *Hyperoodon ampullatus* (Forster, 1770) and *Hyperoodon ampullatus* Flower, 1882. In: Ridgway SH, Harrison RJ (eds) *Handbook of marine mammals, Vol 4*. Academic Press, London, p 321–348
- Newson SE, Mendes S, Crick HQP, Dulvy NK and others (2009) Indicators of the impact of climate change on migratory species. *Endang Species Res* 7:101–113
- Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42
- Perrin WF, Mead JG (1995) Clymene dolphin: *Stenella clymene* (Gray, 1846). In: Ridgway SH, Harrison RJ (eds) *Handbook of marine mammals, Vol 5: the first book of dolphins*. Academic Press, Cambridge, p 161–172
- Perry AL, Low PJ, Ellis JR, Reynolds JD (2005) Climate change and distribution shifts in marine fishes. *Science* 308:1912–1915
- Reeves RR, Smith BD, Crespo EA, Notarbartolo di Sciara G (eds) (2003) *Dolphins, whales and porpoises: 2002–2010 conservation action plan for the world's cetaceans*. IUCN/SSC Cetacean Specialist Group, IUCN, Gland and Cambridge

- Reeves RR, Smeenk C, Kinze C, Brownell RL, Lein J (1999) White-beaked dolphin *Lagenorhynchus albirostris* Gray, 1846. In: Ridgway SH, Harrison RJ (eds) Handbook of marine mammals, Vol 6: the second book of dolphins and the porpoises. Academic Press, Cambridge, p 1–30
- Reyes JC (1996) A possible case of hybridism in wild dolphins. *Mar Mamm Sci* 12:301–307
- Rice DW (1989) Sperm whale: *Physeter macrocephalus* Linnaeus, 1758. In: Ridgway SH, Harrison RJ (eds) Handbook of marine mammals, Vol 4: river dolphins and the larger toothed whales. Academic Press, Cambridge, p 177–234
- Rice DW (1998) Marine mammals of the world: systematics and distribution. Spec Publ No. 4, Society of Marine Mammalogy, Beaufort, NC
- Roberts CM, Hawkins JP (1999) Extinction risk in the sea. *Trends Ecol Evol* 14:241–246
- Simmonds MP, Isaac SL (2007) The impacts of climate change on marine mammals: early signs of significant problems. *Oryx* 41:19–26
- Thomas CD, Cameron A, Green RE, Bakkenes M and others (2004) Extinction risk from climate change. *Nature* 427:145–148
- Tynan CT, DeMaster DP (1997) Observations and predictions of Arctic climatic change: potential effects on marine mammals. *Arctic* 50:308–322
- Walther GR, Post E, Convey P, Menzel A and others (2002) Ecological responses to climate change. *Nature* 416: 389–395
- Watts P, Hansen S, Lavinge DM (1993) Models of heat loss by marine mammals: thermoregulation below the zone of irrelevance. *J Theor Biol* 163:505–525
- Wiens JJ, Graham CH (2005) Niche conservatism: integrating evolution, ecology, and conservation biology. *Annu Rev Ecol Syst* 36:519–539
- Willis PM, Crespi BJ, Dill LM, Baird RW, Hanson MB (2004) Natural hybridization between Dall's porpoises (*Phocoenoides dalli*) and harbour porpoises (*Phocoena phocoena*). *Can J Zool* 82:828–834
- Winn HE, Reichley NE (1985) Humpback whale: *Megaptera novaeangliae*. In: Ridgway SH, Harrison RJ (eds) Handbook of marine mammals. Vol 3: the sirenians and baleen whales. Academic Press, Cambridge, p 241–273
- Zornetzer HR, Duffield DA (2003) Captive-born bottlenose dolphin × common dolphin (*Tursiops truncatus* × *Delphinus capensis*) intergeneric hybrids. *Can J Zool* 81: 1755–1762

Appendix 1. Table A1. Summary of temperature ranges, water depth preferences, climatic category and predicted conservation status due to changes in species' range resulting from climate change for individual marine cetacean species (see Supplement 1 for full species accounts). WWL: warmer water-limited; CWL: cooler water-limited; CWWL: cooler and warmer water-limited

Species	Water temperature preference					Water depth	Climatic category	Predicted conservation implication
	Polar	Sub-polar	Temperate	Sub-tropical	Tropical			
Sperm whales								
Sperm whale	←————→					Oceanic	Cosmopolitan	Unchanged
Pygmy sperm whale	←————→					Oceanic	WWL	Favourable
Dwarf sperm whale	←————→					Oceanic	WWL	Favourable
Beaked whales								
Cuvier's beaked whale	←————→					Oceanic	WWL	Favourable
Arnoux's beaked whale	←————→					Oceanic	CWL	Unfavourable
Baird's beaked whale	←————→					Oceanic	CWWL	Unfavourable
Shepherd's beaked whale	←————→					Oceanic	CWWL	Potentially unfavourable
Longman's beaked whale	←————→					Oceanic	WWL	Favourable
Northern bottlenose whale	←————→					Oceanic	CWL	Unfavourable
Southern bottlenose whale	←————→					Oceanic	CWL	Unfavourable
Hector's beaked whale	←————→					Oceanic	CWWL	Unfavourable
True's beaked whale	←————→					Oceanic	CWWL	Unfavourable
Gervais' beaked whale	←————→					Oceanic	WWL	Favourable
Sowerby's beaked whale	←————→					Oceanic	CWWL	Unfavourable
Gray's beaked whale	←————→					Oceanic	CWWL	Unfavourable
Pygmy beaked whale	←————→					Oceanic	WWL	Favourable
Andrew's beaked whale	←————→					Oceanic	CWWL	Unfavourable
Spade-toothed beaked whale	Unknown					Unknown	Unknown	Unknown
Hubbs' beaked whale	←————→					Oceanic	CWWL	Unfavourable
Ginkgo-toothed beaked whale	←————→					Oceanic	WWL	Potentially favourable
Stejneger's beaked whale	←————→					Oceanic	CWWL	Unfavourable
Strap-toothed beaked whale	←————→					Oceanic	CWWL	Unfavourable
Blainville's beaked whale	←————→					Oceanic	WWL	Favourable
Perrin's beaked whale	Unknown					Unknown	Unknown	Unknown
River dolphins								
Fransiscana	←————→					Shelf	CWWL	Unfavourable
Monodontids								
Beluga	←————→					Shelf & oceanic	CWL	Unfavourable/potentially high risk for some populations
Narwhal	←————→					Shelf & oceanic	CWL	Unfavourable/high risk if Arctic sea ice disappears

Appendix 1 (continued)

Species	Water temperature preference					Water depth	Climatic category	Predicted conservation implication
	Polar	Sub-polar	Temperate	Sub-tropical	Tropical			
Dolphins								
Commerson's dolphin	↔					Shelf	CWWL	High risk
Chilean dolphin	↔					Shelf	CWWL	High risk
Haviside dolphin		↔				Shelf	CWWL	High risk
Hector's dolphin		↔				Shelf	CWWL	High risk
Atlantic humpbacked dolphin			↔			Shelf	WWL	Favourable
Indo-Pacific humpbacked dolphin			↔			Shelf	WWL	Favourable
Tucuxi			↔			Coastal shelf and estuarine	WWL	Favourable
Bottlenose dolphin			↔			Shelf and oceanic	WWL	Favourable
Pan-tropical spotted dolphin			↔			Primarily oceanic	WWL	Favourable
Striped dolphin			↔			Primarily oceanic	WWL	Favourable
Atlantic spotted dolphin			↔			Primarily oceanic	WWL	Favourable
Spinner dolphin			↔			Primarily oceanic	WWL	Favourable
Clymene dolphin			↔			Primarily oceanic	WWL	Favourable
Common dolphin			↔			Oceanic & shelf	WWL	Favourable
Fraser's dolphin			↔			Oceanic	WWL	Favourable
White-beaked dolphin	↔					Shelf	CWWL	Unfavourable/high risk for population around NW Europe
Atlantic white-sided dolphin	↔					Primarily oceanic	CWWL	Unfavourable
Pacific white-sided dolphin	↔					Primarily oceanic	CWWL	Unfavourable
Dusky dolphin			↔			Primarily shelf	CWWL	Unfavourable/high risk for southern Africa population
Peale's dolphin		↔				Shelf	CWWL	High risk
Hourglass dolphin	↔					Primarily oceanic	CWWL	Unfavourable
Northern right whale dolphin	↔					Primarily oceanic	CWWL	Unfavourable
Southern right whale dolphin	↔					Primarily oceanic	CWWL	Unfavourable
Risso's dolphin			↔			Oceanic & shelf	WWL	Favourable
Melon-headed whale			↔			Oceanic	WWL	Favourable
Pygmy killer whale			↔			Oceanic	WWL	Favourable
False killer whale			↔			Oceanic	WWL	Favourable
Long-finned pilot whale	↔					Oceanic	CWWL	Unfavourable/high risk for Mediterranean population
Short-finned pilot whale			↔			Oceanic	WWL	Favourable
Killer whale	↔					Oceanic & shelf	Cosmopolitan	Unchanged
Irrawaddy dolphin			↔			Shelf	WWL	Favourable
Porpoises								
Harbour porpoise	↔					Shelf	CWWL	Unfavourable/high risk for NW European populations
Vaquita			↔			Shelf	Possibly CWL	Potentially high risk
Burmeister's porpoise	↔					Shelf	CWWL	High risk
Spectacled porpoise			↔			Shelf	CWWL	High risk
Finless porpoise			↔			Shelf	WWL	Favourable
Dall's porpoise	↔					Shelf	CWL	Unfavourable
Baleen whales								
Bowhead whale	↔					Oceanic & shelf	CWL	Unfavourable/high risk for Sea of Okhotsk population
Northern right whale	↔					Primarily shelf	CWWL	Unfavourable
Southern right whale	↔					Primarily shelf	CWWL	Unfavourable/high risk for population that breeds in coastal waters of South Africa
Grey whale			↔			Primarily shelf	CWWL	Unchanged
Humpback whale	↔					Shelf & oceanic	Cosmopolitan	Unchanged
Northern minke whale	↔					Shelf & oceanic	Cosmopolitan	Unchanged
Dwarf minke whale			↔			Shelf & oceanic	WWL	Favourable
Antarctic minke whale	↔					Shelf & oceanic	Cosmopolitan	Unchanged
Bryde's whale			↔			Shelf & oceanic	WWL	Favourable
Fin whale	↔					Primarily oceanic	Cosmopolitan	Unchanged
Blue whale	↔					Primarily oceanic	Cosmopolitan	Unchanged
Sei whale	↔					Primarily oceanic	WWL	