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ENVIRONMENTAL STUDIES

Future seasonal changes in habitat for Arctic whales during predicted ocean warming

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Ocean warming is causing shifts in the distributions of marine species, but the location of suitable habitats in the future is unknown, especially in remote regions such as the Arctic. Using satellite tracking data from a 28-year-long period, covering all three endemic Arctic cetaceans (227 individuals) in the Atlantic sector of the Arctic, together with climate models under two emission scenarios, species distributions were projected to assess responses of these whales to climate change by the end of the century. While contrasting responses were observed across species and seasons, long-term predictions suggest northward shifts (243 km in summer versus 121 km in winter) in distribution to cope with climate change. Current summer habitats will decline (mean loss: -25%), while some expansion into new winter areas (mean gain: +3%) is likely. However, comparing gains versus losses raises serious concerns about the ability of these polar species to deal with the disappearance of traditional colder habitats.

INTRODUCTION

Temperature increases projected by global climate models (GCMs) are expected to be amplified in the Northern Hemisphere (1), having substantial consequences for marine life due directly to thermal stress or indirectly to biogeographical shifts and community changes (2, 3). Monitoring community changes throughout the Arctic is technically difficult, but accessible apex predators (e.g., marine mammals) can be used as sentinels for predicting and projecting ecosystem change (4). Numerous changes have been predicted for Arctic endemic cetaceans (bowhead whale, beluga, and narwhal) (5), but to date, the timing of redistributional shifts and the location of future potential habitats for these Arctic species are unknown.

Seasonal association with sea ice is a well-known trait of all three Arctic cetaceans (6–8), and recent studies have demonstrated that the related phenomenon, sea surface temperature (SST), is an important indicator of habitat suitability (9) and is a driver of their movement patterns and population dynamics (10). Because sea ice is expected to continue to decline in the Arctic, SST's role as an indicator of habitat change may be even more crucial in the future. Increasing temperatures may result in range expansions for species that travel between temperate and polar waters (e.g., humpback whale and harbor porpoise), but the range of Arctic species is conversely expected to decline (11). This study predicts the future distribution of the three Arctic cetaceans in the climate-sensitive waters west and east of Greenland (and across the northern Barents Sea), under two climate change scenarios.

A relatively low level of warming has been projected for the area west of Greenland (0.27°C/decade during the 21st century), while stronger warming is expected east of Greenland (0.33°C/decade) and in the Barents Sea (0.50°C/decade) (12). To test whether Arctic cetaceans will respond differently to ocean warming in areas west

and east of Greenland [hereafter West and East (10, 11, 13, 14)], we used a large tracking dataset spanning 28 years, including subpopulations from all three Arctic endemic cetaceans in the Atlantic sector of the Arctic ($n = 227$ whales; fig. S1). Using environmental data from three different GCMs from the Coupled Model Intercomparison Phase 6 (CMIP6), a series of species distribution models were used to (i) estimate current and (ii) predict future (up to 2100) distributions of the three whale species in our study region and to (iii) assess habitat and latitudinal changes in response to global warming.

RESULTS

Model performance

The performance metrics of the three GCMs showed little inter-run variability (SD) and good overall performance (>0.75 , fig. S2). The accuracy of our models varied between 0.70 ± 0.20 (bowheads East in summer) and 0.98 ± 0.16 (narwhals East in summer). The sensitivity varied between 0.55 ± 0.20 (bowheads East in summer) and 0.99 ± 0.002 (narwhals East in summer). The lowest sensitivity was associated with the AWI-CM-1-1-MR climate model for bowhead whales in the West during winter (0.56 ± 0.11), suggesting an underestimation of the presence of this species under this specific model's output. The specificity varied between 0.76 ± 0.06 (bowheads West in summer) and 0.93 ± 0.01 (narwhals East during winter).

Summer projections

The summer distribution of belugas during the current period shows two main aggregations located north and south of Baffin Island (Fig. 1, top row). In 2100, our models project a loss of habitat associated with a northern migration under scenario ssp126, while under ssp585, a complete loss of habitat is expected for this species (Figs. 1 and 2, top rows).

Bowhead whales are found largely in coastal areas in the West and in areas with pack ice (>200 km) north of Svalbard eastward to Franz Joseph Land (Fig. 1, middle row). Between the present and 2100, our models project a northerly shift of key habitats in summer, simultaneous with a significant contraction in habitat for both sides, with the most marked habitat loss suggested under scenario ssp585 (Figs. 1 and 2, middle row).

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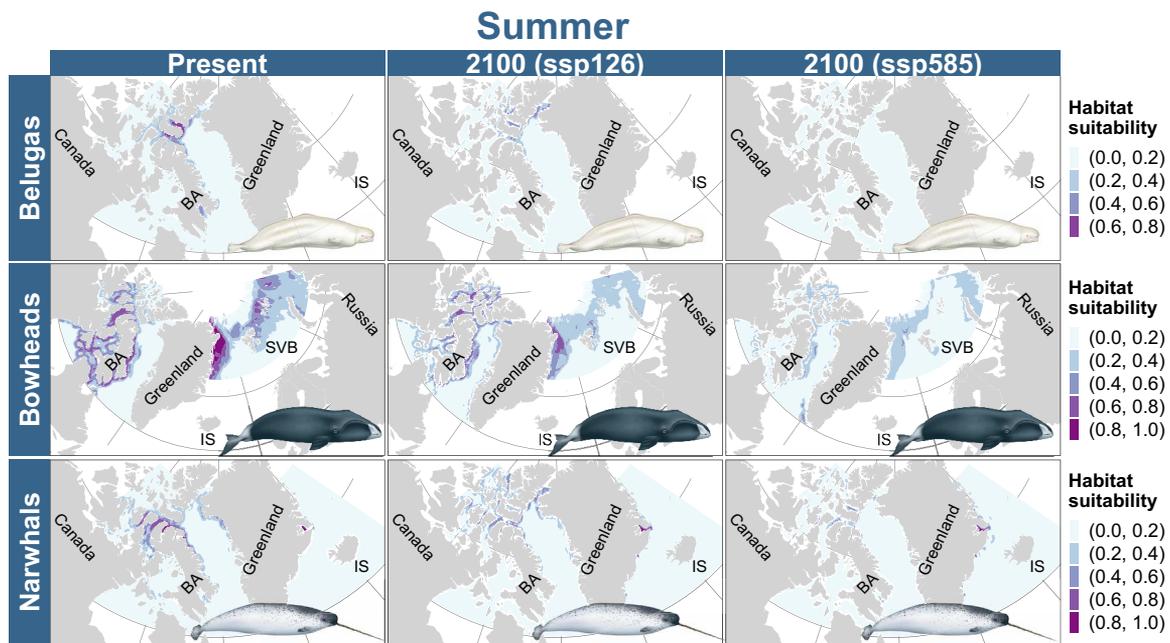


Fig. 1. Predictive maps of habitat suitability for belugas, bowhead whales and narwhals for the present and for 2100 in summer (August to September) for both scenarios (ssp126 and ssp585). “BA” corresponds to Baffin Island, “IS” to Iceland, and “SVB” to Svalbard. Cetacean illustrations by Uko Gorter.

In summer, narwhals now occupy most of northern Baffin Bay in the West and a tight coastal strip along Greenland in the East (Fig. 1, bottom row). Except for narwhals in the East, predictions by 2100 indicate a notable habitat loss in summer, with the most pronounced loss under scenario ssp585 (Figs. 1 and 2, bottom row). Intermodel variability is shown in fig. S4.

Winter projections

In winter, our models project a northwestward expansion of bowhead whales’ habitat in the West (Fig. 3, top row) into the Canadian Arctic Archipelago (Fig. 4, top row). In the East, while bowheads will lose most of their current habitat under the ssp585 scenario, ssp126 projects some new habitat becoming available further north (Fig. 4, top row).

Narwhals are expected to lose a significant portion of their current winter habitat by 2100 in the West, especially under scenario ssp585 (Figs. 3 and 4, bottom rows). In the East, they are expected to experience a complete loss of their offshore wintering habitat (Figs. 3 and 4, bottom rows). Intermodel variability is shown in fig. S5.

Habitat change

Except for narwhals in the East, projected habitats are expected to decrease in summer for all species and for both scenarios (Fig. 5A). The models project an average decline between -71% (SD, ± 17.5 , ssp126) and -88% (± 23.6 , ssp585) in available habitat for belugas, -28% (± 53.7) and -68% (± 15.3) for bowhead whales, and -31% (± 56.9 , ssp126) and -66% (± 27.2 , ssp585) for narwhals West. In summer, narwhals East are expected to gain habitat area between 85% (± 67.0 , ssp126) and 105% (± 114.0 , ssp585).

In winter, projected habitats on average expected to decrease for narwhals but increase for bowhead whales at least in the West; in the East, little change is predicted, and the direction of change varies

under the two climate scenarios (Fig. 5B). Projected habitat decline for narwhals varies between -10% (± 23.6 , ssp126, narwhals West) and -63% (± 41.9 , ssp585, narwhals East). Expected habitat gain for bowheads in winter ranged between 7% (± 36.8 , ssp126, bowheads East) and 80% (± 135 , ssp585, bowheads West). For bowhead whales, only the East side, under scenario ssp585, shows an average loss of habitat by 2100 ($-9 \pm 48.0\%$).

Northward shift

A northward shift was projected in both summer and winter habitats for all three Arctic endemic species, ranging from 37 ± 44 km (narwhals West in winter, ssp126) to 475 ± 261 km (bowheads West in summer, ssp126; see Fig. 6). The northward shift was less pronounced in winter (122 ± 84 km) compared to summer (243 ± 142 km, Kruskal-Wallis rank sum test, $P = 0.06$).

DISCUSSION

By combining satellite tracking and climate models, our study sheds light on the projected habitat changes of subpopulations of the three endemic Arctic whale species under distinct climate change scenarios. Although a common trend was observed across the geographically isolated subpopulations, intra- and interspecific variations are expected to occur, including contrasting responses across seasons.

Except for narwhals in the East, substantial habitat loss is projected for the three species in summer, regardless of which climate scenario is used. Belugas now have a broad north-south range, but they are divided into small local populations that exhibit high site fidelity, which makes them vulnerable to environmental change. Most beluga populations in the North Atlantic region are now small (15, 16), including the one in southeast Baffin Island tracked in this study (16). Climate change is already thought to be a factor that is limiting recovery of

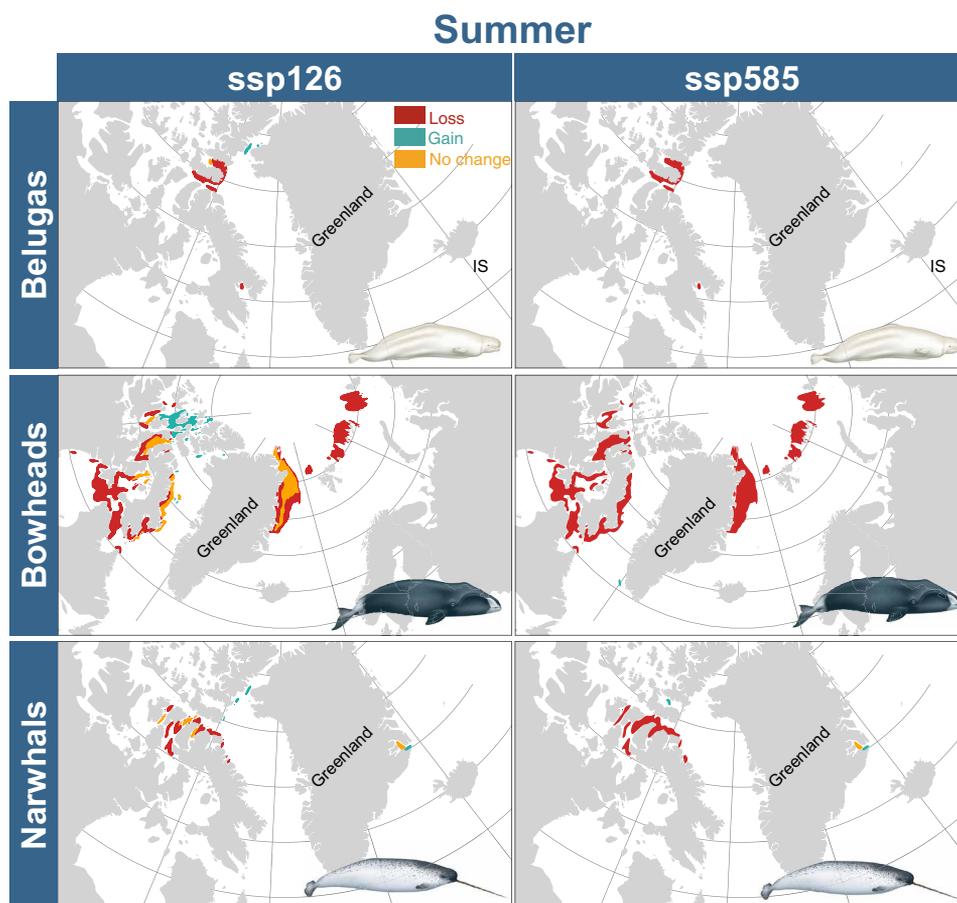


Fig. 2. Changes in projected summer core habitats (probabilities >0.5) by the year 2100 for the three Arctic whale species for both scenarios. Red areas are projected losses by 2100, orange areas are expected to remain unchanged, and green areas are projected increases in habitat. Cetacean illustrations by Uko Gorter.

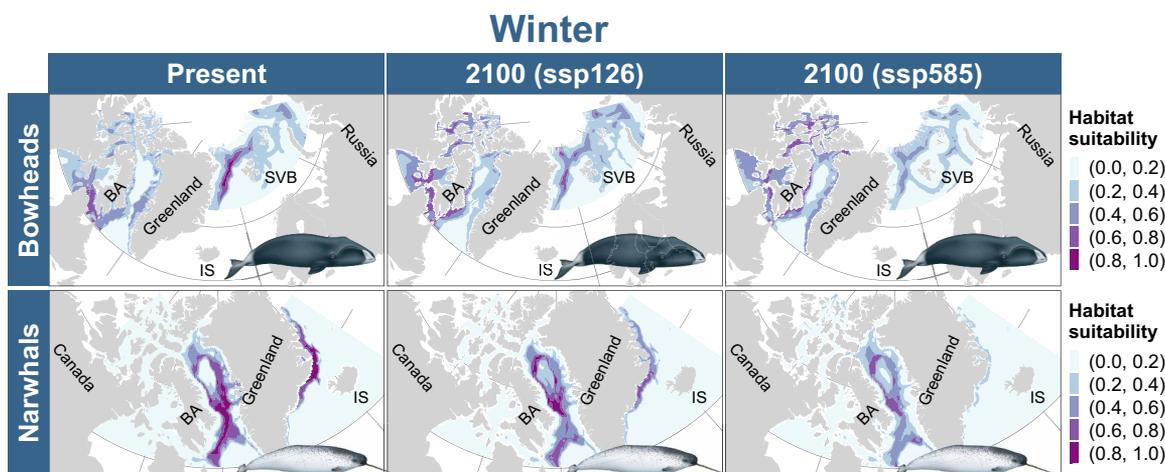


Fig. 3. Predictive maps of habitat suitability for bowhead whales and narwhals for the present and for 2100 in winter (December to March) for both scenarios (ssp126 and ssp585). Not enough data were available to model belugas in winter. Cetacean illustrations by Uko Gorter.

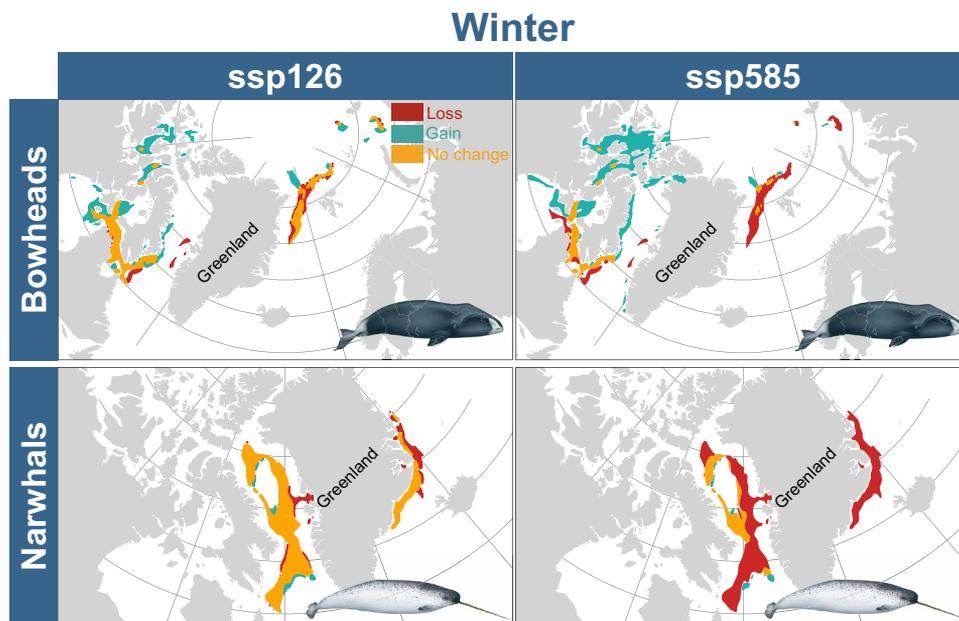


Fig. 4. Changes in projected winter core habitats (probabilities >0.5) by the year 2100 for bowhead whales and narwhals for both scenarios. Not enough data were available to model belugas in winter. Red areas are projected losses by 2100, orange areas are expected to remain unchanged, and green areas are projected increases in habitat. Cetacean illustrations by Uko Gorter.

these populations from previous overexploitation (14), and because belugas show strong site fidelity to summering grounds, they will likely not move, despite the expected habitat deterioration.

Bowhead whales are now found largely in coastal areas in the West and in areas with pack ice (>200 km) north of Svalbard eastward to Franz Joseph Land, well north of their historical range. Few sightings occur around Svalbard where bowheads were abundant during the Little Ice Age (1300 to 1860), before the near extirpation of the Spitsbergen stock by commercial whaling (17). Loss of sea ice in the Canadian Arctic Archipelago due to rising temperatures will allow bowhead whales to remain year-round in small refugial areas. Historically, these areas were used intensively by bowhead whale hunters from the Thule culture during a warm period some 1000 years ago (18). In East Greenland, bowhead whales are already found further north than their historical range (13); however, there is a limit to how far north they can move without losing contact with important pelagic zooplankton prey resources that benefit from upwelling along the continental shelf edge.

Narwhal distributions north of the current range might be feasible, given that narwhals are deep divers that might be able to feed on mesopelagic prey in deeper waters of the Arctic Ocean. Traditional migration patterns for some stocks, strong site fidelity, and their natural tendency to at least seasonally affiliate with sea ice might however limit their adaptability to such new habitats. In contrast to summer, most current wintering habitats are projected to disappear for narwhals in the East. Population numbers for narwhals have been reduced in both the West (particularly in Melville Bay) and throughout their range in the East, where the situation for the species is already dire (10, 19). The narwhal is recognized as one of the most sensitive species of Arctic marine mammals to climate change (5) due to its reliance on sea ice, restricted niche, limited range, specialized diet, and complex population structure (20, 21). Over the least severe scenario (ssp1226), climate change would make current ice-covered

areas increasingly accessible in West Greenland and Canada, generating new habitats for Arctic whales. However, under the most severe scenario (ssp585), habitat in the West is predicted to exist only in small areas north of Baffin Island in summer, which have been predicted to be the last Arctic summer ice refugia (22).

One potential limitation to our study is that not all Arctic endemic whale populations in the study region were included in the sample of tracked animals, due to logistical challenges with tracking whales from small, remote populations. Two subpopulations of belugas are included in the current study. Three other Arctic subpopulations, in Hudson Bay, the White Sea, and Svalbard, were not included. The latter two, because they are stationary year-round, are likely to have similar responses to what our models predicted. Data are lacking for the Hudson Bay subpopulation. Regarding narwhals, seven subpopulations have been included in our analysis and five stocks are missing [Northeast Greenland, East Baffin, Hudson Bay, Smith Sound, and Jones Sound; see (10)]. Most of these are logistically difficult to get information from, but we believe that they would follow the same response to climate change as shown for the tagged stocks. For bowhead whales, there are now two distinct stocks in the Atlantic sector of the Arctic, and both have been included in our dataset. Modeling the distribution of a species is needed at the subpopulation level to capture intraspecific variability (23), as shown by the contrasting responses that we observed between West and East Greenland in our study. Although habitat relationships may vary geographically, the current climate models available from CMIP6 do not allow for detection of subtle environmental changes at a fine scale (<25 km), reinforcing the assumption that the missing stocks would respond similarly to the populations used in our study. Unsourced populations of belugas and narwhals, with more southerly distributions than those included in this study, are almost certain to face reductions in habitat similar or larger to those documented for the northern populations.

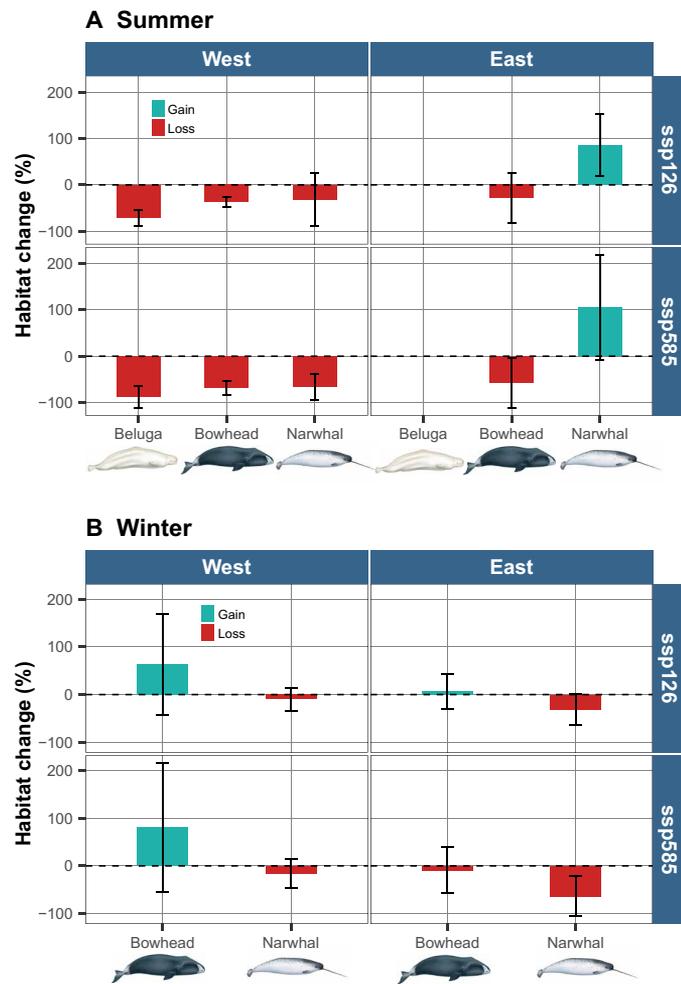


Fig. 5. Barplots of the habitat change predicted (average \pm SD) for Arctic whale species in summer and winter for both scenarios. Habitat change refers to the difference between the area of current suitable habitat and the area of projected habitat in 2100, i.e., a positive change means that the habitat has expanded (in green), and negative change means that the habitat has contracted (in red). Cetacean illustrations by Uko Gorter.

Sea ice was not included as a potential driver of the whales' distributions because climate models project a complete disappearance of sea ice in summer by 2060 (24) and because sea ice is nearly absent in the foraging grounds of many of the Arctic endemic cetaceans in summer already. Sea ice is also highly correlated with SST, which is included in our models as a key predictor. Another factor not directly assessed by our models was potential changes in prey biomass and abundance that may affect local habitat conditions. The effects of fine-scale changes in prey availability on the behavior and distribution of marine top predators are difficult to project, especially at high latitudes given the lack of prey data for these remote locations. Many Arctic species have a conservative niche selection and have, like the three endemic whale species, little plasticity when it comes to changes in habitat selection.

Our models are correlative rather than mechanistic, excluding physiological processes. However, it is assumed that the consequences of climate change will affect apex predators directly by acting on their physiology through alterations in thermoregulatory costs and

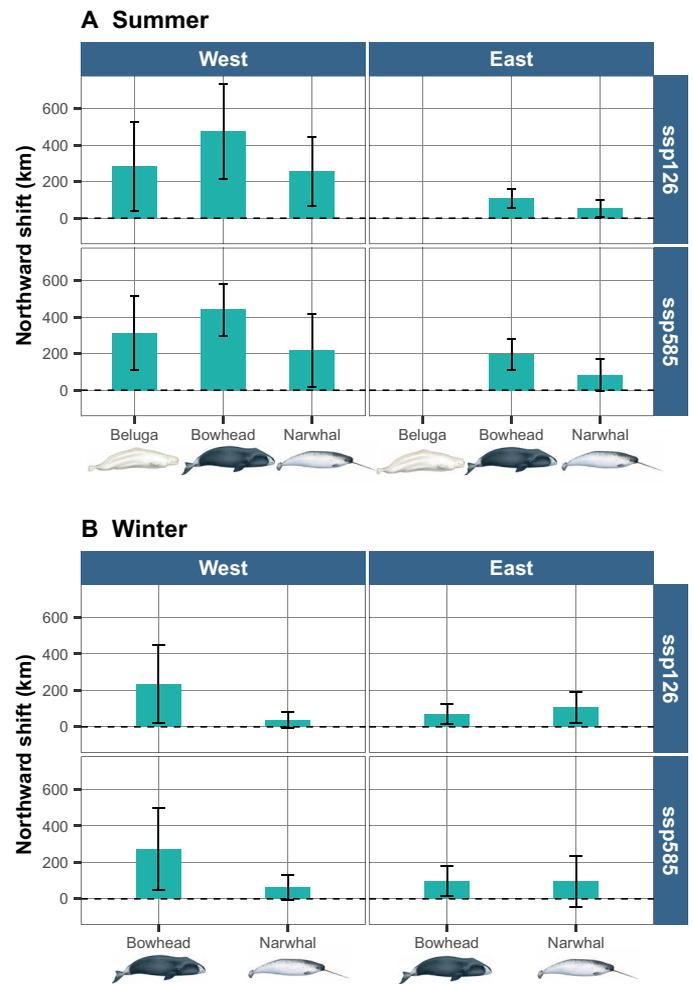


Fig. 6. Barplots of the northward shift predicted (average \pm SD) for Arctic whales in summer and winter for both scenarios. The northern shift is the difference between the current average latitudinal range and the average projected latitudinal range in 2100 (expressed in kilometers). Cetacean illustrations by Uko Gorter.

perhaps also metabolic processes (25). When suitable physiological data become available, the use of Arctic cetaceans as sentinels for habitat changes could be improved by combining spatial, behavioral, and physiological information to generate even more accurate predictions.

For deep divers that forage at great depth, surface environmental variables almost certainly do not fully reflect suitable habitats. However, to date, projected changes in sea temperature and salinity at depth show a certain level of inconsistency when historical simulations are compared to observational climatology (26). In addition, the foraging depths of these animals are not fully elucidated for all subpopulations. Recent advances show that narwhals might forage mainly below 300 m, because buzzing activity is much higher at these depths (27), but for belugas and bowheads, such data are not available yet, making projections in depth unpredictable.

Despite some variability across the climate models in summer, the average projected response (in terms of habitat and latitudinal changes) was similar across most of the models and species. However, in winter, the intermodel variability was higher, showing contrasting

responses for some species, especially bowheads West. Shen *et al.* (28) recently showed that climate models from CMIP6 have a smaller intermodel spread in climatological sea ice extent in the Arctic compared to CMIP5 during summer months, which could explain why our winter projections are more heterogeneous. Because of uncertainties related to projections, in particular in the Arctic (29), it is essential to apply an array of climate models when projecting the future responses of marine species to climate change. We were limited in our study by the small number of climate models available at a fine scale (25 km), but we recommend combining additional models for future studies conducted in the Arctic, once additional fine-scale models will become available.

By assembling a large, multispecies dataset for the three Arctic cetaceans including 227 individuals, our study sheds light on the predicted habitat changes and distributional shifts that these cold-adapted species might undertake in response to an imminent global warming scenario. Because conditions at the southern limits of their current range will no longer meet their ecological needs or encompass their preferred metabolic temperature tolerances (20), these Arctic species are expected to lose a significant proportion of their current habitat and disperse toward higher latitudes. Boreal species (e.g., killer whale, humpback whale, and harbor porpoises) are also expected to migrate northward (30), increasing the risk of interspecific competition to access marine resources, as well as predation levels, making Arctic species even more vulnerable. In line with a recent study conducted in the Southern Ocean (31), our findings help identifying Areas of Ecological Significance using marine megafauna species as bioindicators of the state of marine resources. These apex predators play an important role in structuring the entire ecosystem and regulating the marine food web. Like other ecosystems, the Arctic is now facing an increasing number of anthropogenic stressors, including climate change and resource exploitation. During the ice-free season, seismic surveys are being conducted in the Arctic at ever increasing rates, resulting in noise disturbance for the marine life, especially for whales that communicate acoustically over large distances and rely on echolocation to hunt prey and navigate in deep waters (for toothed whale species). With melting sea ice, new routes are becoming available to ship traffic, increasing the frequency and intensity of noise pollution on these animals (32). Behavioral responses to air gun pulses and ship noise have recently been demonstrated for narwhals (33, 34). Consequently, the expected rise in sea temperature might affect not only the geographical range of these Arctic species but also their space use (35), phenology (36), abundance (10), foraging success (37), and survival rate (38), raising serious concerns about how these cold-adapted species will cope with anthropogenic stressors originating from both resource exploitation and climate change.

MATERIALS AND METHODS

Study areas and tag deployment

The study used a large dataset including tracking data from belugas ($n = 29$), bowhead whales ($n = 71$), and narwhals ($n = 129$) tagged in two domains: west and east of Greenland, extending into the Barents Sea for bowhead whales (Table 1 and fig. S1). This dataset covers 28 years (from 1993 to 2020) with locations collected from field campaigns conducted on belugas West, bowhead whales, and narwhals West and East. Capture and tagging procedures are described in (10, 13, 39).

Location processing

Data were relayed through the Argos Data Collection and Location System and decoded using Argos Message Decoder (DAP version 3.0, build 114, Wildlife Computers). The filtering approach of Albertsen *et al.* (40) was applied to the tracking data to improve the Argos locations accuracy. GPS-based positioning (i.e., Fastloc technology) was not filtered. On the basis of seasonal movement patterns previously documented for the three study species (10, 13, 39, 41), two periods were selected to depict the whales' seasonal distributions: summer (August to September) and winter (December to March; fig. S1). To get a representative picture of the whales' distributions, individuals with less than 50 locations were excluded from the analyses. Years with tracks of less than two individuals within a species were also discarded.

Species distribution modeling

To identify the environmental drivers of the whales' movements and to predict their potential distributions and project their future distribution under two climatic scenarios, we built a series of species distribution models following a six-step procedure as follows (fig. S3).

Data preparation

First, an environmental background-based technique was used to generate pseudo-absences (42), relying on the assumption that true absences are more likely located in areas that are environmentally dissimilar from presence locations. A two-dimensional environmental background was generated representing the ordination results of the environmental variables available over the study area. SST, mixed layer depth (MLD), sea surface height (SSH), and sea surface salinity (SSS) were used as potential drivers of the whales' distributions. The four dynamic predictors were extracted monthly in summer (August and September) and winter (December to March) at the whales' locations and pseudo-absences in each particular month and year from the following three GCMs from the CMIP6: AWI-CM-1-1-MR, CNRM-CM6-1-HR, and HadGEM3-GC31-MM. These three GCMs were chosen on the basis of their fine spatial resolution (25 km) compared to other GCMs. Historical data from each of the three GCMs were extracted for the four variables over the whales' tracking period (1993 to 2020). Bathymetry, extracted from the General Bathymetric Chart of the Oceans (GEBCO) (resolution 30 arc sec, ~1 km grid) was also retained as a potential environmental predictor of the whales' movements (43). Because of the coastal movements of some of the whales, especially within the fjords in summer, we also used the distance to shore as a key variable using the *distancetocoast* package (<https://mdsummer.github.io/distancetocoast/>).

Pseudo-absences were then randomly generated outside environmentally favorable areas for each season and each individual, in equal numbers to the filtered occurrences (e.g., tracking locations). To increase the robustness of the results and assess their sensitivity to the pseudo-absences generation procedure, 10 different sets of pseudo-absences were simulated (i.e., 10 runs for each season). The environmental variables were then extracted at each occurrence along with pseudo-absences. The obtained binary dataset (presence/absence) was then split into training (70%) and test (30%) datasets for each run. To avoid overly optimistic model outputs and reduce spatial autocorrelation, distinct spatial folds were generated on the basis of the identity of each whale using the *CAST* package (44).

Model training

Seven algorithms from the *caret* package in R were then used to model presence of the whales from the training dataset using the six environmental predictors. To find the model that predicted the distribution

Table 1. Summary of the tracking dataset used in the study including the two sectors (West and East Greenland) for the three cetacean species. Note that some individuals contribute to both the summer and winter season; the total number of individuals tracked was 227.

Season	Species	Location	N individuals	N locations	Period
Summer	Beluga	West	29	8,956	1995–2001
	Narwhal	West	69	26,497	1993–2012
	Narwhal	East	54	37,988	2010–2019
	Bowhead	West	56	19,216	2002–2019
	Bowhead	East	12	4,705	2017–2019
Winter	Narwhal	West	28	15,493	1994–2009
	Narwhal	East	36	19,945	2010–2020
	Bowhead	West	9	4,620	2005–2011
	Bowhead	East	10	5,014	2017–2020

of the whales with the highest performance, we tested seven different algorithms belonging to the following categories: “Ensemble” (random forest, boosted tree, and gradient boosting machine), “Regression” (boosted generalized additive model, boosted generalized linear model, and multivariate adaptive regression splines), and neural network. The seven algorithms were run for each simulation ($n = 10$) and each GCM ($n = 3$) using the presence of the whales (1: presence versus 0: pseudo-absence) as a response variable. Collinearity of the predictors was checked using the variance inflation factor (below four), and all predictors were centered and scaled. A forward feature selection was used from the CAST package to select the most important variables by testing all possible two-pair combinations, improving model performance (44).

Model selection

Model comparison was based on a fourfold cross-validation conducted on the test dataset for each run and each GCM using accuracy, sensitivity, and specificity as the performance metrics (table S1 and fig. S2). Model selection was based on the three performance metrics and on a visual inspection of the prediction maps from each GCM. Average yearly maps were generated on the basis of the 10 predictions derived from the 10 runs for each species and each location (West and East) and each GCM separately to account for potential inter-GCM variability.

Model tuning

Once the best algorithm was chosen for each species and locality, the model hyperparameters were tuned to increase the performance. This was done for each GCM and each season, separately.

Predictions of the current distribution

Yearly seasonal predictions from the tuned model were generated and then averaged for each species from each locality to provide a final map of the potential distribution of Arctic whales for each GCM, separately. To provide a global map of current habitats considering the three GCMs, an average prediction map was then generated from the three GCMs per season. Maps of the SDs derived from the three GCMs were also generated to account for the intermodel variability (figs. S4 and S5).

Projections of the future distribution

Data from the projected variables (SST, SSS, SSH, and MLD) were extracted monthly from the same GCMs between 2020 and 2100 under two Shared Socioeconomic Pathways (SSPs): the most optimistic scenario SSP126 (scenario assuming a warming below 2°C)

and the high-forcing scenario SSP585 (retaining a strong reliance on fossil fuels in the future). Climatic projections of the future distributions of the three species were generated using these forecast maps. Habitat change (expressed in percentage) was estimated as the difference between the area covered by current suitable habitat (probability >0.5) and projected habitat in 2100 (probability: >0.5). The 0.5 threshold was chosen to be representative of the most suitable core habitat while excluding areas that might be potentially unsuitable (<0.5). Although a threshold of 0.5 can lead to biased predictions in case of imbalanced datasets, because we deal with a prevalence of 50%, the 0.5 threshold appears to be the most robust approach (45, 46). Similarly, the latitudinal change was assessed by calculating the northern movement of the whales (expressed in km), i.e., difference between the current average latitudinal range and the average projected latitudinal range in 2100.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <https://science.org/doi/10.1126/sciadv.abn2422>

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