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A SPECIES DISTRIBUTION MODEL OF THE ANTARCTIC MINKE WHALE (*BALAENOPTERA BONAERENSIS*)

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Balaenoptera bonaerensis, Southern Ocean, species distribution modelling, Bayesian additive regression trees, biological indicator, climate change

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Abstract

The Antarctic minke whale (*Balaenoptera bonaerensis*) is regarded a Southern Hemisphere endemic found throughout the Southern Hemisphere, generally south of 60°S in austral summer. Here they have been routinely observed in highest densities adjacent to and inside the sea ice edge, and where they feed predominantly on krill. Detecting abundance trends regarding this species by employing visual monitoring is problematic. Partly this is because the whales are frequently sighted within sea ice where navigational safety concerns prevent ships from surveying. In this respect species-habitat models are increasingly recognized as valuable tools to predict the probability of cetacean presence, relative abundance or density throughout an area of interest and to gain insight into the ecological processes affecting these patterns. The objective of this study was to provide this background information for the above research needs and in a broader context use species distribution models (SDMs) to establish a current habitat suitability description for the species and to identify the main environmental covariates related to its distribution. We used filtered 464 occurrences to generate the SDMs. We selected eight predictor variables with reduced collinearity for constructing the models: mean annuals of the surface temperature (ºC), salinity (PSS), current velocity (m/s), sea ice concentration (fraction, %), chlorophyll-a concentration (mg/m³), primary productivity (g/m^3/day), cloud cover (%), and bathymetry (m). Six modelling algorithms were tested and the Bayesian additive regression trees (BART) model demonstrated the best performance. Based on variable importance, those that best explained the environmental requirements of the species were sea ice concentration, chlorophyll-a concentration and topography of the sea floor (bathymetry), explaining in sum around 62% of the variance. Using the BART model, habitat preferences have been interpreted from patterns in partial dependence plots. Areas where the AMW have particularly high likelihood of occurrence are East Antarctica, NE of the Weddell Sea, areas around the northern tip of the Antarctica Peninsula, areas bordering the Scotia–Weddell Confluence. Given the association of AMWs with sea ice, the pagophilic character of their biology makes them particularly vulnerable to climate change and a near-perfect biological indicator for tracking these changes.

Cite as

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Комп'ютерна модель поширення антарктичного смугача (*Balaenoptera bonaerensis*)

Володимир Титар

Резюме. Антарктичний смугач (*Balaenoptera bonaerensis*) є ендеміком південної півкулі, зустрічається, як правило, на південь від 60° пд. ш. влітку. Тут їх зазвичай спостерігають біля краю морської криги та посеред неї, де вони харчуються переважно крилем. Виявити тенденції чисельності цього виду за допомогою візуального моніторингу проблематично. Частково це пов'язано з тим, що китів часто бачать посеред морської криги, де проблеми безпеки навігації заважають кораблям проводити спостереження. У цьому відношенні комп'ютерні моделі екологічної ніші все більше визнаються цінними інструментами для прогнозування ймовірності присутності китоподібних, відносної чисельності або щільності на території, що представляє інтерес, а також для отримання уявлення про екологічні процеси, що впливають на поширення цих тварин. Мета цього дослідження полягала в тому, щоб отримати інформацію для зазначених дослідницьких потреб і в ширшому контексті використати комп'ютерні моделі поширення видів (SDM) для встановлення того, наскільки придатне для існування виду те чи інше середовище, та визначення основних параметрів останнього, які цьому сприяють. Для створення SDM ми використали 464 відфільтрованих реєстрацій та вибрали вісім мало скорельованих предикторів: середньорічні значення температури поверхні моря (ºC), солоність (PSS), швидкість течії (м/с), концентрація морської криги (частка, %), концентрація хлорофілу-а (мг/м³), первинна продуктивність (г/м^3/добу), хмарність (%) та батиметрія (м). Було протестовано шість алгоритмів моделювання, і модель байєсівських адитивних регресійних дерев (BART) продемонструвала перевагу над іншими. За моделлю, основними чинниками, які формують нішу виду є: концентрація морської криги, концентрація хлорофілу-а та рельєф морського дна (батиметрія), що в сумі пояснює близько 62% дисперсії. Райони, де смугачі мають особливо високу ймовірність перебування, — це Східна Антарктида, райони на північний схід від моря Уедделла, води навколо північної окраїни Антарктичного півострова, райони, що межують із злиттям вод морів Уеддела та Скоша. Враховуючи зв'язок смугачів з морською кригою, пагофільний характер їхньої біології робить їх особливо вразливими до зміни клімату і тому цей вид є майже ідеальним біологічним індикатором для відстеження цих змін.

Ключові слова: *Balaenoptera bonaerensis*, Південний океан, моделювання поширення видів, байєсівські адитивні регресійні дерева, біологічний індикатор, зміна клімату

Introduction

Minke whales are the smallest of the balaenopterid whales and two species of minke whales are recognized, the common minke whale, *Balaenoptera acutorostrata*, and the Antarctic minke whale (AMW), *B. bonaerensis*. The AMW is regarded a Southern Hemisphere endemic [Deméré 2014] and is found throughout the Southern Hemisphere, generally south of 60°S in austral summer, where they have been routinely observed in highest densities adjacent to and inside the sea ice edge [Williams *et al.* 2014; Herr *et al.* 2019], and where they feed predominantly on krill [Friedlaender *et al.* 2006]. The AMW is considered pagophilic in the sense of being better able than the larger baleen whales to use habitat with high pack ice densities. AMWs have small, compact bodies, and short fins, making them well suited to life in the pack ice where they can easily maneuver in narrow spaces between ice floes [Ainley *et al.* 2007]. Hard, pointed rostrums also allow minke whales to break through thin ice to breathe, creating holes, which in turn may provide an ecological service to other air-breathing marine predators such as seals and penguins [Ainley *et al.* 2007; Tynan *et al.* 2009]. Predator avoidance too has been suggested as another reason for AMWs to use sea-ice habitats, inaccessible to Type A killer whales [Pitman & Ensor 2003].

Deriving precise and unbiased estimates of abundance of cetacean species in the Antarctic region is central for understanding population trends. In the case of the AMW, populations are still being impacted by ongoing commercial whaling carried out against the backdrop of global climate change and other anthropogenic impacts [Risch *et al.* 2019]. However, detecting abundance trends regarding this species by employing visual monitoring from boats, ships or airplanes, one of the most common approaches to study marine mammal distribution and abundance [e.g. Barlow 2015], is problematic. Partly, this is because the whales are frequently sighted within Antarctic sea ice where navigational safety concerns prevent ships from surveying [Williams *et al.* 2014]. Despite recent advances in visual monitoring methods [Ferguson *et al.* 2018], these approaches are yet limited and can only provide a snapshot of the true distribution, particularly for far-ranging species such as minke whales [Kaschner *et al.* 2012]. Nevertheless, current population estimates and their trend raise concerns and accordingly have resulted in the recent classification of the AMW as Near Threatened under the IUCN Red List and under Appendix I of CITES [Cooke *et al.* 2018].

In this respect quantitative species-habitat models are increasingly recognized as valuable tools to predict the probability of cetacean presence, relative abundance or density throughout an area of interest and to gain insight into the ecological processes affecting these patterns [Hammond *et al.* 2013; Robinson *et al.* 2017; Fiedler *et al.* 2018; Melo-Merino *et al.* 2020]. By fitting models of presence or abundance to relevant environmental variables, and then projecting them into geographic space, dynamic responses to environmental variability can be predicted [Becker *et al.* 2018]. Predictions from these models can also be used to develop and evaluate management and conservation strategies [Fiedler *et al.* 2018] and provide a basis for adaptive surveys or sampling design as effort could be concentrated in areas predicted to have greater abundance [Becker *et al.* 2012] and/or higher habitat suitability assumed to be correlated with the species' abundance [Chavez-Rosales *et al.* 2019]. In our specific case we believe there is an opportunity, by exploring present relationships between the AMW and a number of oceanographic covariates, including sea ice concentration, to distinguish such areas of potential high habitat suitability regardless of logistic constraints and in the long run help to build more robust abundance estimates for the species. The objective of this study was to provide this background information for the above research needs and, in a broader context, use species distribution models (SDMs) to establish a current habitat suitability description for the cetacean species and to identify the main environmental covariates related to its distribution.

Materials and Methods

There is a large number of cetacean sighting records from an array of platforms, reflecting presence-only records, which, together with readily available and broad-scale environmental data, provide an opportunity to improve our knowledge of the distribution of the AMW using species distribution modelling. Presence data was retrieved from online public databases, which were accessed using the R package 'spocc' version 0.9.0 [Chamberlain 2018], supplemented from Ukrainian sources and recent updates [Savenko 2020] obtained around or nearby the Akademik Vernadsky Ukrainian Antarctic station. Only point records south of 60°S were considered. As required by SDM software, each cetacean sighting was treated as a single presence record, independent of the number of animals sighted. To reduce both spatial bias and spatial autocorrelation in occurrence data, we performed a spatial thinning procedure by selecting only one presence point within each pixel of the predictor variable maps using SAGA GIS [Conrad *et al.* 2015]. Because true absence data is not available, we used pseudo-absence points randomly generated within a bounding box encompassing AMW presence points by employing the 'dismo' R package [Hijmans *et al.* 2011].

Cetacean occurrence is usually modelled against a range of topographic, physical, and oceanographic factors [Breen *et al.* 2016]. Since cetacean distributions may primarily be driven by those of their prey, it is likely that such factors serve as proxies for spatio-temporal variation in prey density [Baines & Weir 2020]. We used the R package 'sdmpredictors' version 0.2.9 to access potential predictor variables for current projections available for the study area [Bosch 2020]. We chose the Bio-ORACLE version 2.0 dataset [Assis *et al.* 2018]. These variables represent temperature, salinity, chlorophyll concentration, and current velocity, among other factors. Present values refer to the period between 2000 and 2014. Variables were available at a spatial resolution of 5 arc-minutes. Bathymetry was included as a topographic layer derived from the ETOPO1 Global Relief Model [Amante & Eakins 2009]. All the environmental layers were processed in SAGA GIS in datum WGS84, with the same spatial extent and the same resolution.

Because collinearity among environmental variables may lead to overfitting, we used Spearman rank correlation coefficients in the 'caret' R package [Kuhn 2008] to exclude redundant variables with significant correlation coefficients ($|r_s| > 0.8$) from the analyses.

There is a large suite of algorithms available for modelling the distribution of species, but because there is no single 'best' algorithm some authors have reasonably suggested that niche or distribution modelling studies should begin by testing a suite of algorithms [e.g. Qiao *et al.* 2015]. Accordingly, we assessed the relative performance of commonly used SDM algorithms based on envelope and statistical models, and machine learning techniques: BIOCLIM [Busby 1991; Booth *et al.* 2014], generalized linear models [Guisan *et al.* 2002], Maxent [Phillips *et al.* 2006], random forests [Breiman 2001] and boosted regression trees [Elith *et al.* 2008]; these were employed using the 'sdm' package within the statistical software R [Naimi & Araújo 2016]. In addition, we tested Bayesian additive regression trees (BART), a relatively new alternative to other popular classification tree methods, having yet to find a wider application in predicting species distributions, and based on inductive learning process carried out using the Bayes theorem. For running SDMs with BARTs, we used the recently developed 'embarcadero' R package [Carlson 2020]. As part of their output, most algorithms rank the environmental layers used to train the SDM based on their relative importance in building the models. Importantly, they also allow the construction of response curves to elucidate the effect of selected variables on habitat suitability [Phillips & Dudik 2008]. Of particular interest are patterns in partial dependence plots, which are plots of the marginal effect of a predictor variable when other variables are held constant [Pearson 2020]. Models were evaluated by 10-fold cross-validation using 20% of the occurrence dataset.

The AUC (area under the curve) was used to assess the predictive performance of the models [Hosmer & Lemeshow 1989]. Models with mean test-AUC values of AUC<0.7 are considered of poor predictive performance, 0.7≤AUC<0.8 moderate, and AUC≥0.8 good to excellent performance [Duan *et al.* 2014]. Presently, there is a discussion about the reliability of AUC to measure the performance of models based on presence-only methods [Lobo *et al.* 2008; etc.], therefore to have a complementary measure of model performance we calculated the true skill statistic (TSS) [Allouche *et al.* 2006]. The TSS can assume values between −1 and 1 and values of TSS<0.2 can be considered as reflecting poor model predictive performance, 0.2≤TSS<0.4 as fair, 0.4≤TSS<0.6 moderate, and TSS≥0.6 as good to excellent performance. However, model selection based solely on discriminatory ability, without consideration of overfitting, tends to result in overly complex models [Radosavljevic & Anderson 2014]. In this respect, overfitted models will often produce jagged response curves that likely appear to be modelling noise, rather than biological response [Tobeña *et al.* 2016]. Model robustness and reliability were assessed by comparing model results to the current knowledge of AMW ecology and distribution.

We used the 10th percentile training presence threshold value to generate contour lines separating suitable areas from unsuitable [Liu *et al.* 2005]. This threshold value provides a better ecologically significant result when compared with more restricted threshold values [Phillips & Dudík 2008].

Results and Discussion

After filtering the presence data consisting of 1022 georeferenced records, we used 464 occurrences to generate the SDMs. We selected eight predictor variables with reduced collinearity for constructing the models. These represent mean annuals of the surface temperature (ºC), salinity (PSS), current velocity (m/s), sea ice concentration (fraction, %), chlorophyll-a concentration (mg/m^3), primary productivity (g/m^3/day), cloud cover (%), and bathymetry (m).

The outputs of the SDM algorithms varied in terms of discrimination accuracy evaluated by the AUC and TSS (Table 1). According to these results, the Bayesian additive regression trees model demonstrates the best performance (AUC = 0.88, TSS = 0.66), very closely followed by the random forests model (AUC = 0.88, TSS = 0.65). To make a choice between them we inspected the covariate response curves generated by both models in terms of 'smoothness.'

SDM methods	AUC	TSS
BIOCLIM	0.70	0.37
Generalized Linear Model	0.78	0.50
Maxent	0.83	0.60
Random forests	0.88	0.65
Boosted regression trees	0.82	0.57
Bayesian additive regression trees	0.88	0.66

Table 1. Discrimination accuracy of employed SDM algorithms

Таблиця 1. Точність дискримінації використаних алгоритмів

In this respect, the random forests model suggested overfitting, therefore the Bayesian additive regression trees algorithm was selected to perform an in-depth analysis of the niche of the AMW in relation to the selected environmental predictors and the distribution of the species in the Antarctic region. In addition, the package ‘embarcadero’ includes an automated variable selection procedure being highly effective at identifying informative subsets of predictors, allows to generate and plot partial dependence curves.

The modelling identified a number of environmental variables that mostly contributed to generating the potential distribution prediction of the AMW in the study area. Based on variable importance, those that best explained the environmental requirements of the species were sea ice concentration, chlorophyll-a concentration and topography of the sea floor [bathymetry], explaining in sum around 62% of the variance.

Using the BART model, habitat preferences can be interpreted from patterns in partial dependence plots, where predicted habitat suitability is plotted against a marginal change in each variable, all other variables set to their average value.

Firstly, we analyse sea ice concentration preferences. As mentioned, the species is pagophilic and observed densities of the AMW are the highest near the edge of the pack ice, likely because occurrences are typically recorded from observations made on ships unable to penetrate sea ice, but advanced surveys had shown that the AMW also occurs inside the ice pack and within polynyas [Williams *et al.* 2014]. The proportion of the population found within the pack ice is not well known but has been estimated, for instance, at 10–50% in the south-east Indian Ocean sector in summer [Kelly *et al.* 2014] and up to 20% of AMWs of the Weddell Sea were within ice covered waters [Williams *et al.* 2014].

In a relatively recent study, satellite telemetry from three individuals revealed AMW summer foraging spaces can generally be associated with pack ice habitat, delimited by the sea ice extent (SIE), over the continental shelf [Lee *et al.* 2017]. SIE defines the ocean area covered by sea ice and a threshold of minimum sea ice concentration (15%) is used to identify the SIE [Worby & Comiso 2004], although others [Zhao *et al.* 2015] consider it to be 13%. In the study conducted by Lee and co-authors [2017], one whale remained in pack ice concentrations greater than 50%. The other followed the coastline and the SIE as it travelled through the Bellingshausen and Amundsen seas, predominantly within 50 km of the SIE. This whale remained in low ice concentrations, less than 50%, for its entire foraging season.

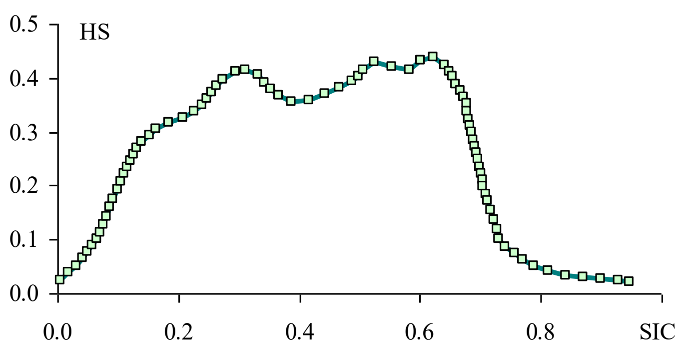

Fig. 1. Partial response curve, SIC = sea ice concentration (%), HS = habitat suitability.

Рис. 1. Крива парціального відгуку стосовно концентрації морської криги, SIC = концентрація морської криги (%), HS = придатність середовища перебування.

The partial response curve, considering the association between habitat suitability (HS) and sea ice concentration (SIC) (Fig. 1), shows that in both cases the individuals most likely were in preferable areas where SICs best match their niche requirements. Starting from a threshold of minimum sea ice concentration of 15%, HS with increasing SIC demonstrates a sharp rise with a more or less steady growth trend towards a concentration of 60%, after which it rapidly declines, indicating predominantly unsuitable habitat. On the whole, SICs between 30 to 60% seem, according to the model, to be mostly favoured by the species. Using the 10th percentile training presence threshold value (HS = 0.245) suitable areas, in terms of SIC, occupy a wider range from around 12 to 69%, that is to say areas moderately off the SIE to areas considerably packed with ice.

A recent report of occurrences throughout the full range of ice concentrations found AMW densities generally lower in high ice concentrations [Herr *et al.* 2019]. Likely, in the pursue of krill closely linked with the under-ice environment [Nicol 2006], AMWs reach their prey under the ice in places extending from 27 km beyond the ice edge [Brierley *et al.* 2002] up to hundreds of kilometres into the ice-covered area, as in the Lazarev Sea [Flores *et al.* 2012] and other parts of the Southern Ocean [Herr *et al.* 2019], as far as there are regions of open water (such as leads, polynyas etc.). In this respect, AMWs exploit a unique niche among sympatric whale species feeding on krill in the Southern Ocean [Friedlaender *et al.* 2014].

Secondly, since cetacean distributions may primarily be driven by those of their prey, it is likely that such factors as chlorophyll-a concentration serve as proxies for spatio-temporal variation in prey density [Baines & Weir 2020]. Indeed, the corresponding partial response curve (Fig. 2) shows a steep rise of HS between concentrations 0.8 and 1.0 mg/m³, reaching an unprecedented value of almost 90% at the chlorophyll-a concentration of 1.35 mg/m³. Using the employed threshold value, suitable conditions are expected to appear above the concentration of 0.6 mg/m³.

Next in the row of influential variables is ocean depth. It has been documented that the distribution of AMWs is related to the continental shelf break [Ainley *et al.* 2012]. The corresponding curve for ocean water depth (Fig. 3) showed a sharp positive response with areas shallower than approximately 3000 m (using a Maxent model, authors cited above consider it to be around 3500 m), reaching a maximum at around 1000 m, a mark close to the continental shelf break, slightly declining and rising once again as the distance to the shore decreases.

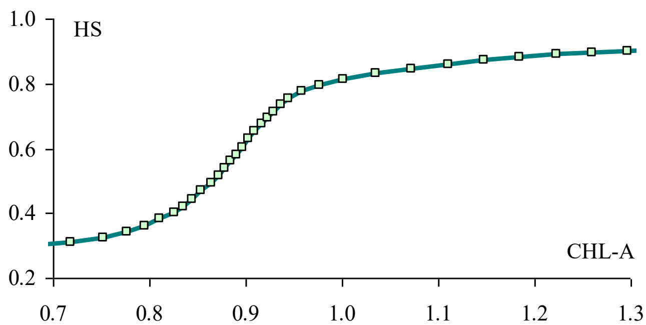

Fig. 2. Partial response curve, CHL-A = chlorophyll-a concentration (mg/m³).

Рис. 2. Крива парціального відгуку стосовно концентрації хлорофілу-а, CHL-A = концентрація хлорофілу-а (мг/м³).

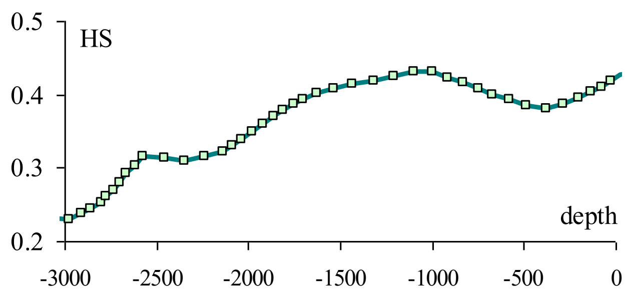

Fig. 3. Partial response curve, DEPTH = depth below zero [km].

Рис. 3. Крива парціального відгуку стосовно глибини моря, над яким перебувають смугачі, DEPTH = глибина від поверхні (км).

Once again, referring to the study conducted by Lee and co-authors [2017], two of the tracked whales demonstrated bimodal distributions in bathymetry, remaining in the shallow waters of the continental shelf early in the season and moving into deeper water as the season progressed, a behaviour which appears to be consistent with our model. Generally speaking, the shelf break is defined as the line between the shelf and the upper continental slope. Around Antarctica, the ice load and the resulting isostatic equilibrium and erosion result in a deep shelf. Some authors consider the shelf break to be mostly located between 400 and 600 m water depth [Arndt *et al.* 2013], others around 800 m [Murase *et al.* 2013] or 1000 m [Atkinson *et al.* 2008].

Our model indicates that the shelf break and shelf waters inshore of it seem to be areas with the habitats attractive to the AMW and where higher densities of the species have been recorded [Herr *et al.* 2019]. The importance of the vicinity of the shelf break area in various locations throughout the Southern Ocean is that Antarctic krill, a dominant prey item for AMWs, occurs here in higher densities [Siegel & Watkins 2016]. Using the employed threshold value, suitable conditions should appear in waters shallower that 2790 m, but the best being around 800–1000 m and/or in nearshore habitats.

The combination of sea ice concentration, chlorophyll-a concentration, and bathymetry in the present study's model appears to successfully predict the presumed foraging habitat and distribution for the AMW (Fig. 4). Areas where the AMW have particularly high likelihood of occurrence are East Antarctica, NE of the Weddell Sea, areas around the northern tip of the Antarctica Peninsula, areas bordering the Scotia–Weddell Confluence.

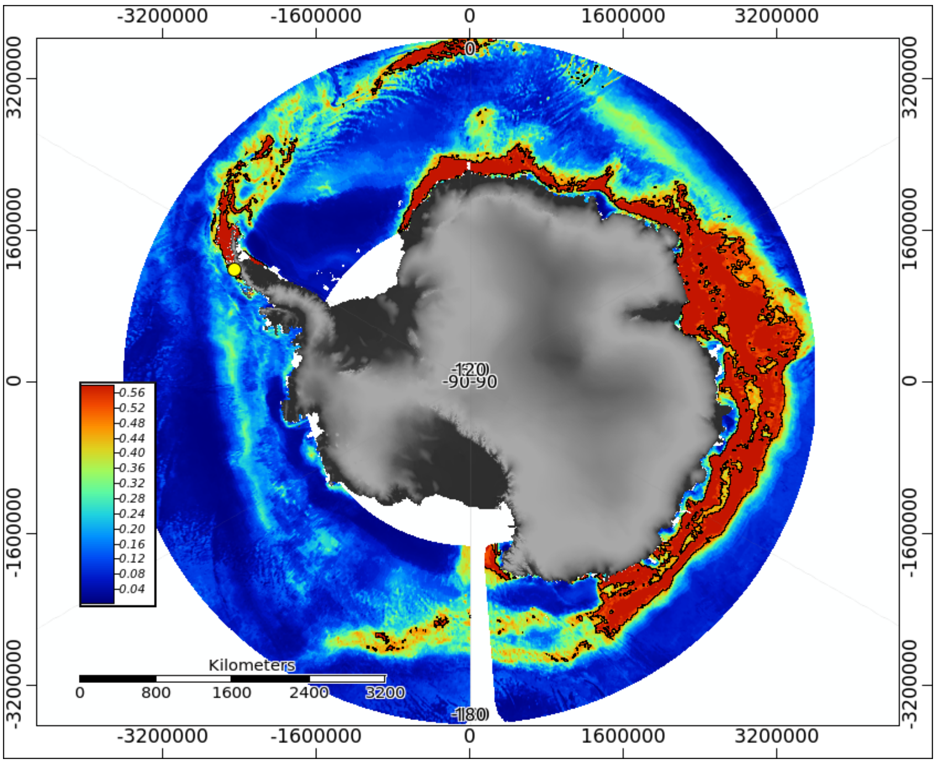

Fig. 4. Result of the Bayesian additive regression trees [BART] modelling: modelled habitat suitability for Antarctic minke whales in the Southern Ocean. Warmer colours indicate better habitat suitability. Yellow dot: Akademik Vernadsky Ukrainian Antarctic station.

Рис. 4. Результат моделювання за алгоритмом байєсівських адитивних регресійних дерев (BART): модель регіонів Південного океану придатних для перебування антарктичних смугачів. Тепліші кольори вказують на регіони з більш придатними для тварин умовами. Жовтий кружечок показує місце розташування Української антарктичної станції «Академік Вернадський»

Conclusions

The spatial distribution of biological organisms is one of the fundamental pieces of information necessary to understand their ecology. Detailed current knowledge of the distributions of cetaceans and their suitable habitat is important for the effective management and conservation not only of cetacean species but also of entire marine ecosystems [Kanaji *et al.* 2015].

The application of presence-only SDMs for marine species is particularly attractive due to often logistical and economic costs of obtaining systematic species' distribution data [Smith *et al.* 2021]. Exploring present relationships between AMW and environmental variables can highlight potential reasons for shifts in abundance estimates and help to build more robust survey methods for the future [Williams *et al.* 2014], provide a basis for adaptive surveys or sampling design as effort could be concentrated in areas predicted to have better habitat suitability.

Suitable habitat for AMWs predicted by the SDM is interpreted as regions where the species is most likely to be found, and represent priority areas where monitoring efforts (including passive acoustic monitoring and aerial and/or vessel-based surveys) should be focused in the coming years. Given the pagophilic character of the biology of AMWs, this makes them particularly vulnerable to climate change and a near-perfect biological indicator for tracking these changes.

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