Sea-ice anomalies affect the acoustic presence of Antarctic pinnipeds in breeding areas

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Sea ice is crucial for breeding in true Antarctic pinnipeds. Although critical to interpret and mitigate the effects of extreme climatic events on polar species, knowledge of the effects of strong sea-ice anomalies on the reproductive activity of true Antarctic pinnipeds is scarce. Underwater vocalizations in these species play a key role in reproduction and function as indicators for presence and breeding onset. Using 8 years of recordings, we quantified the effect of sea-ice concentration and drift on the acoustic presence probability of four pinniped species in their breeding areas. In all four species, acoustic activity timing was constant across years, but decreased when sea-ice cover conditions were <10%, suggesting that individuals may fail to anticipate rapid changes in sea-ice cover. In the species' traditional breeding areas, extreme and regular negative anomalies in early austral-summer sea ice could affect long-term reproductive success. Our findings underscore the urgent need for a better understanding of climate-driven changes in high-fidelity breeding areas to mitigate current and future anthropogenic pressures, and to sustain the integrity and functionality of the Southern Ocean's ecosystems.

Front Ecol Environ 2023; 21(5): 227–233, doi:10.1002/fee.2622

Humans have directly modified 87% of the world's oceans (Watson *et al*. 2018), but the Southern Ocean encircling Antarctica constitutes one of the Earth's last relatively pristine marine wildernesses on Earth. Nevertheless, as with much of the rest of the natural world, Southern Ocean ecosystems are increasingly under pressure from climate change (eg Gutt *et al*. 2021), resulting in such physical changes as rising ocean temperatures and global reductions in sea-ice extent (Swart *et al*. 2018; Stammerjohn and Scambos 2020). At the same time, stronger and sometimes opposing regional fluctuations in sea-ice extent and seasonality are occurring; in the Ross Sea, sea-ice extent and seasonal sea-ice duration have increased by 4.5–5% per decade and ~2.4 days per year, respectively, whereas both have decreased by 5–6% per decade and ~3.1 days per year, respectively, west of the Antarctic Peninsula (Stammerjohn *et al*. 2012). Consequently, the effects of climate-induced changes on marine biota in the Southern Ocean may vary regionally, and will strongly depend on the ecological role that the area fulfills for species of interest.

Many Antarctic migratory and resident marine species, including marine mammals, seabirds, and zooplankton, depend on sea ice for reproduction and even survival (eg Nicol *et al*. 2008; Meyer *et al*. 2017; Trathan *et al*. 2020). True Antarctic pinniped species are those that rely on sea ice as haul-out platforms and are bound to species-specific sea-ice characteristics for breeding (Siniff 1991). Therefore, the timing of many phases in pinniped life histories is tightly coupled to the availability and quality of the species-specific sea-ice habitat (Siniff 1991; Southwell *et al*. 2003). However, the role of shifts in sea-ice habitats for true Antarctic pinnipeds has to date been primarily explained in terms of consequences for their foraging habitats and food availability (eg Hadley *et al*. 2007; Siniff *et al*. 2008; Hückstädt *et al*. 2020). Research has nevertheless largely neglected to directly quantify the relationship between variability in sea-ice cover, as physical support for breeding and haul-out, and the reproductive activities of ice-breeding species. This knowledge gap likely reflects the logistical challenges of surveying animals in polar regions using traditional methods, and the consequent lack of baseline data on population trends and life-history parameters for true Antarctic pinnipeds. This pressing lack of knowledge currently impedes interpretation and mitigation of the impacts of climate change and extreme events on polar (pinniped) species.

True Antarctic pinnipeds are aquatic mating (Van Parijs 2003) and therefore information about the location, timing, and duration of reproductive behaviors can be derived from their vocal presence and activity (Van Parijs 2003; Van Opzeeland *et al*. 2010). Here, we used passive acoustic monitoring (PAM) data covering an 8-year period over which large fluctuations in sea-ice cover occurred to quantify the relationship between the acoustic presence probability of four Antarctic pinnipeds – Weddell seal (*Leptonychotes weddellii*), Ross seal (*Ommatophoca rossii*), leopard seal (*Hydrurga leptonyx*), and crabeater seal (*Lobodon carcinophaga*) – in the reproductive season and local sea-ice characteristics (including sea-ice concentration, drift velocity, and drift direction) across years. Specifically, we examined how strong negative anomalies in austral-summer sea-ice cover conditions in a true Antarctic pinniped breeding area affected the timing and amount of pinniped acoustic activity.

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Methods

Long-term passive acoustic data

PAM data were collected by the Perennial Acoustic Observatory in the Antarctic Ocean (PALAOA) (see also Van Opzeeland *et al.* 2010), situated on the edge of the Eckström Ice shelf in the Atlantic Section of the Southern Ocean (Figure 1). We analyzed continuous recordings made from 2007 to 2014 that were collected with an active RESON TC4032 hydrophone suspended in the water column 70 m beneath the ice shelf (~160 m thick) and 90 m above the seafloor. Recordings were originally compressed to MP3 streams at 192 kilobits (kBits) per second into 1-minute files with 32 kilohertz (kHz) sampling rates and 16-bit depths, making for a total of 3,173,989 files (>4 terabytes) (see WebTable 1). The effective bandwidth of the recordings was 10 hertz (Hz) to 15 kHz, with a dynamic range of 60–150 decibels referenced to a pressure of one micropascal (generally shortened to dB re 1 μPa).

Acoustic data processing and acoustic metrics

To obtain a better resolution for the calls of the true Antarctic pinniped species, we decimated (a process that entails lowpass-filtering and reducing the sampling rate of the signal) the acoustic files to 7 kHz sampling rate using the R (v4.0.3) packages *monitoR* (Hafner and Katz 2018), *seewave* (Sueur *et al.* 2008), and *tuner* (Ligges *et al.* 2018) (R Core Team 2020). We stratified our random sampling to build a training set ($n = 1535$) that comprised quality recordings (signal-to-noise ratio [SNR] > 1 dB and ≥ 1 complete call) that covered the call repertoire of the species and optimized the inclusion of temporal variability across the study period. We assessed species acoustic presence/absence from spectrograms (Raven Pro 1.5, Cornell Lab of Ornithology, Ithaca, NY) of 1-minute files by visually and aurally identifying species-specific calls and matching the signatures to existing call libraries (see also Van Opzeeland *et al.* 2010). To parameterize species' call patterns and train classification models, we automatically computed 41 standardized acoustic metrics on every 1-minute file in the dataset (see WebTable 2 for a detailed list).

Random forest classification models

We trained random forest classification models (Breiman 2001) to discriminate between the acoustic presence/absence of the four pinniped species recorded off PALAOA using the *randomForest* function of the R package *randomForest* (Liaw and Wiener 2002). We ran a full-hyperparameter grid search for each species model to identify the best model parameterization to stabilize prediction error rates and used the out-of-bag error to estimate the overall misclassification rate of the model. Using the *Boruta* function of the R package *Boruta* (Kursa and Rudnicki 2010), we applied the Boruta algorithm to select relevant acoustic metrics to include as predictor variables in the classification model by iteratively removing the variables that were statistically less relevant to the classification accuracy than their randomly permuted copies.

To cross-validate the species presence probabilities predicted by the random forest models for each 1-minute file across the entire dataset, we randomly selected 3200 acoustic files, creating an independent test set. We manually assessed the species acoustic presence/absence in the test set following the training set protocol. We used the *optimal.threholds* function of the R package *PresenceAbsence* (Freeman and Moisen 2008) to calculate optimal thresholds for species presence/absence predictions. A threshold was exclusively applied

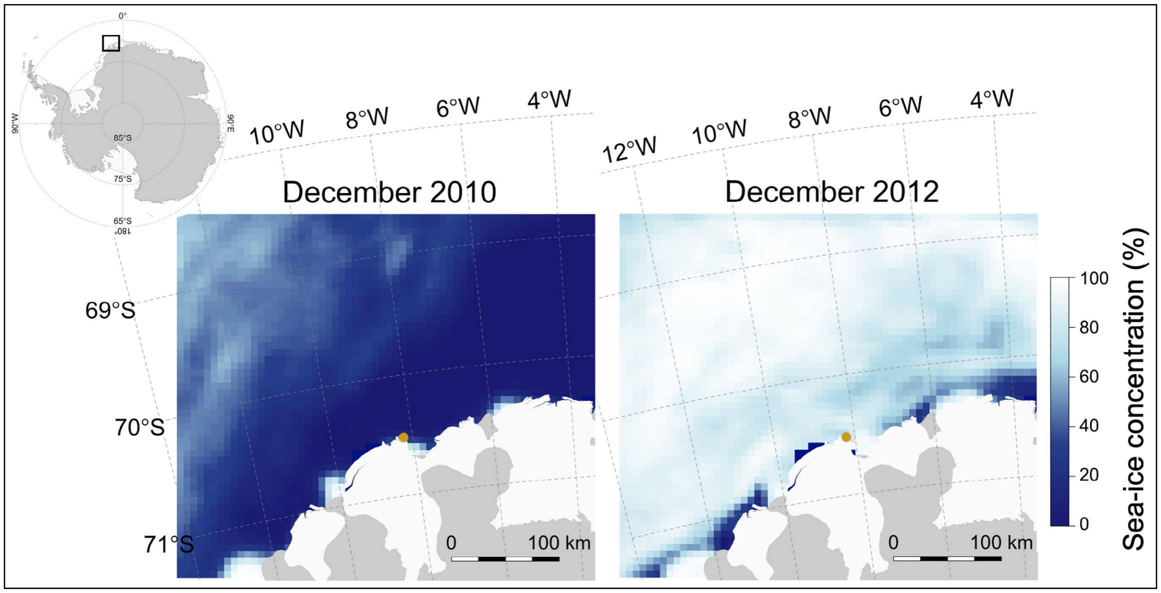

Figure 1. Maps of the study area off the Perennial Acoustic Observatory in the Antarctic Ocean (PALAOA, depicted by the yellow circle) and average sea-ice cover in December 2010 and December 2012.

to model predictions to evaluate model performance and to compute the species relative daily proportion of acoustic presence (or acoustic activity). This relative acoustic activity was computed as the sum of the 1-minute species presence scores per day (obtained by applying the optimal threshold to the estimated probabilities) divided by the total number of minutes virtually recorded per day (ie 1440 and 24 for March–December 2013). When interpreting the variation in relative proportion, the imbalance in the number of files available per year/month in the dataset must be accounted for (WebTable 1). We used the *confusionMatrix* function of the R package *caret* (Kuhn *et al*. 2020) to conduct the second-step evaluation of model performance.

Environmental predictors

We used daily sea-ice concentration (SIC) data retrieved with the ARTIST sea-ice (ASI) algorithm (Spreen *et al*. 2008) applied to microwave radiometer data from the sensors AMSR-E (Advanced Microwave Scanning Radiometer for EOS, on the Aqua satellite) and AMSR2 (Advanced Microwave Scanning Radiometer 2, on the GCOM-W1 satellite) (both with a resolution and grid size of 6.25 km), as well as to data from the sensor SSMIS (Special Sensor Microwave Imager/Sounder, on the DMSP-F17 satellite) (with interpolation applied to match the 6.25-km grid size). Data from the SSMIS were used to replace the missing AMSR-E derived sea-ice maps after the latter instrument's failure in April 2011–July 2012. However, due to inconsistencies between the AMSR and SSMIS data (WebFigure 1), the AMSR gap period was omitted in the regression models. In addition, we obtained daily values of sea-ice drift (overall sea-ice velocity, *v* [vertical] and *u* [horizontal] components of ice motion) (Tschudi *et al*. 2019) for the 2007–2014 period, at 25-km resolution. We extracted daily point values for SIC and drift from an area within a 30-km radius around PALAOA using the *extract* function of the R package *raster* (Hijmans 2020). The radius length represented the probable distance over which pinniped calls were detected at PALAOA and therefore the estimated range of representative ice conditions to which the pinnipeds recorded off PALAOA were exposed to (Shabangu and Rogers 2021). For SIC and sea-ice drift velocity, we calculated the spatial average and standard deviation across the daily point values within the 30-km-radius area, along with the daily drift direction as north-based azimuth values (0–360°) using the *v* and *u* sea-ice drift components.

Relationship between model estimates and sea-ice conditions

To test the effect of the sea-ice predictors on pinniped acoustic presence probabilities, we fitted one generalized additive model (GAM) (Wood 2017) per species. GAMs included data exclusively from the time period in which the acoustic activity of each species was observed – year-round for Weddell seals and 2–3 months for the seasonal seal species (WebTable 3). We included daily averaged estimates of species acoustic presence probability as the dependent variable and daily (spatial aggregates) SIC, sea-ice drift velocity, and sea-ice drift direction as continuous fixed-effects predictors. SIC standard deviation and drift velocity standard deviation were also included as fixed terms as a measure of spatial variability in SIC (accessibility to floes of pack ice: large, continuous ice masses formed by the accumulation of smaller pieces of free-floating ice) and in sea-ice drift velocity, respectively. To account for the underlying ecological differences during specific time periods, we included – as random effects (intercept) – nested *year* and *month* in the model for the Weddell seal and *summer-season* (one summer season per year) in the models for the other three Antarctic pinniped species. Smooths for single variables were fitted using thin plate regression splines, with the exception of sea-ice drift direction, which was modeled as a cyclic smooth term to account for equivalency of its range's end points. We used the *gam* function of the R package *mgcv* (Wood 2017) and a beta regression parameterization to account for the mathematical bound (0–1) of the probability values (Ferrari and Cribari-Neto 2004). We relied on maximum likelihood (as a smoothing parameter estimation method) and the model's explained deviance (to evaluate model fit). The estimated effective degrees of freedom (edf) were used as a proxy for the degree of nonlinearity in the relationship between acoustic probability and the SIC predictors (Zuur *et al*. 2009). We used the function *dredge* of the R package *MuMIn* (Bartoń 2020) to evaluate all possible fixed-effect term combinations and excerpt relative model weight based on the Akaike information criterion (Burnham and Anderson 2002). We then applied the *importance* function of the *MuMIn* package to assign a relative strength of evidence (importance) to each independent term.

Results and discussion

Classification model performance

We provide the first applied example of random forest classification models trained with standardized/automated metrics to predict the long-term acoustic presence of a pinniped community. Models were successful at accurately estimating the presence and absence of the true Antarctic pinniped species recorded off PALAOA across years, while trained with complex, non-preprocessed (non-filtered) soundscapes in which inter- and intraspecific vocalizations concurred (WebTables 3 and 4). The second-step evaluation of classification models' performance showed high specificity and negative predictive values (>0.80) for all species and, in general, good sensitivity (0.70–0.62) and precision scores (0.85–0.66), except for the crabeater seal, the model for which exhibited lower sensitivity at this step (WebTable 5). The Ross seal classification model incorrectly estimated some minor acoustic activity during the winter period in 2009 and 2013, which was manually verified. When the classification model predictions were aggregated to the day level (Figure 2), model estimations on the general timing of the four species' intra-annual acoustic activity concurred with the observed prevalence (WebTable 3) and previous short-term year-round observations in the Weddell Sea (eg Van Opzeeland *et al.* 2010). These results reinforce the suitability of these model-based estimations as a tool to overcome the labor-intensive analysis of PAM data and the use of PAM to explore patterns in long-term dynamics for the effect of environmental drivers (including climate-driven changes) on marine acoustic communities.

The sea-ice environment off PALAOA

Median SIC levels off PALAOA generally exceeded 75% during winter (April–October) and early summer months (November–December), and exceeded 25% from January to April across the studied period. However, from early December 2010 through January 2011, SIC levels displayed a particularly strong negative anomaly, with medians of less than 10% SIC (Figures 1 and 2). Mean summer sea-ice extent over the eastern Weddell Sea is in general strongly determined by loss of sea-ice cover in early summer; once established in December (as was the case in 2010), large negative sea-ice anomalies persist over the summer, leading to warming of the ocean surface and subsequent sea-ice melt (Turner *et al.* 2020). Indeed, summer 2010–2011 exhibited one of the lowest mean sea-ice extents in the eastern Weddell Sea as compared to the late 20th-century record, matched only by the negative anomalies reported since 2016 (reflecting the ongoing warming trend) (Stammerjohn and Scambos 2020; Turner *et al.* 2020).

Sea-ice variation, drift, and Antarctic pinnipeds' acoustic presence probability

Overall, across years, the sea-ice environment strongly influenced the acoustic presence probability of the studied pinniped species. Along with SIC, both SIC standard deviation and sea-ice drift velocity were the most important predictors of the acoustic presence probability of the pinniped species in their traditional breeding areas (Figure 3). The lowest model fit was that for leopard seal, suggesting that other factors (possibly the presence of potential prey species) may also influence the distribution and acoustic activity of this species (Rogers 2009).

Spatial variation in SIC serves as a proxy of sea-ice accessibility for swimming individuals: the higher the SIC variability, the more accessible ice floes are for seals (Wege *et al.* 2021b). In the coastal region we focused on, the greatest variation in SIC occurred at intermediate and low SIC levels. We found a negative effect of SIC variation on Weddell seal acoustic presence probability, likely reflecting this species' preference for fast ice (sea ice attached to the coast, the seafloor, or a grounded object, such as an iceberg) (Siniff 1991). At the same time, Ross and leopard seal acoustic presence probability exhibited positive relationships with the SIC variability. Given that, during summer, breeding and molting seals also exploit near-shelf areas as foraging grounds (Wege *et al.* 2021a,b), higher SIC variability may benefit these species through both easier access to sea-ice floes for haul-out and increased nearby foraging

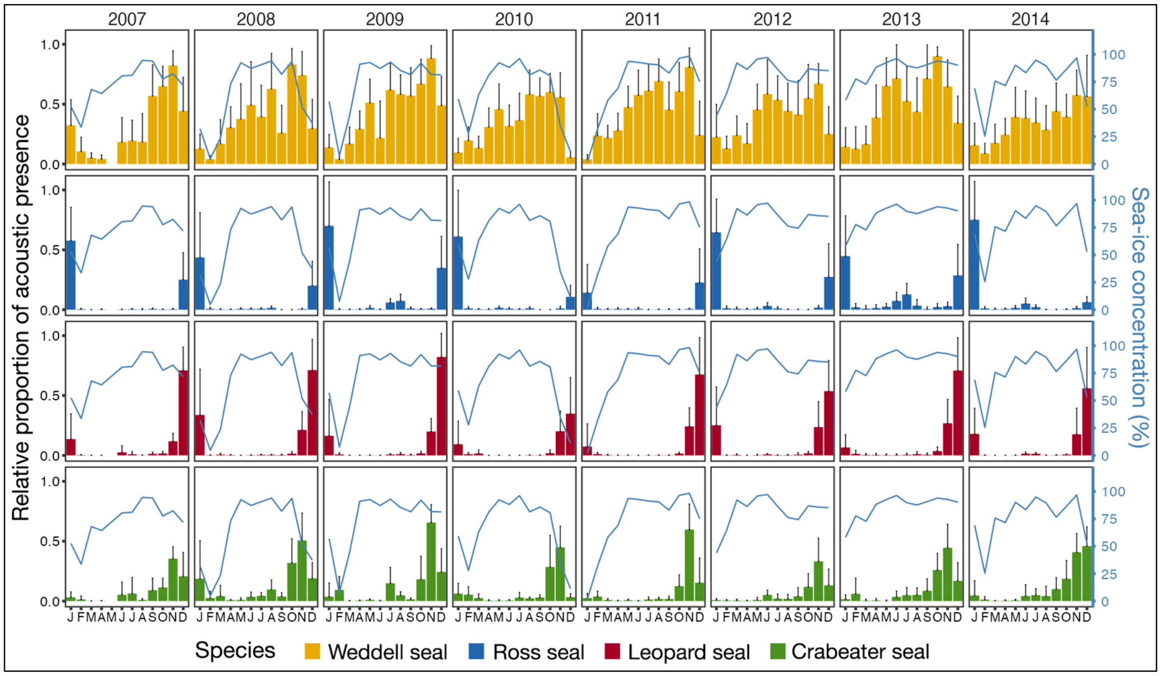

Figure 2. Predicted acoustic activity of four true Antarctic pinniped species recorded off PALAOA and sea-ice concentration (SIC) from 2007 to 2014. Colored bars and error bars show the monthly average and standard deviation, respectively, in the relative daily proportion of species' acoustic presence. The blue line represents the monthly SIC average within 30 km around PALAOA.

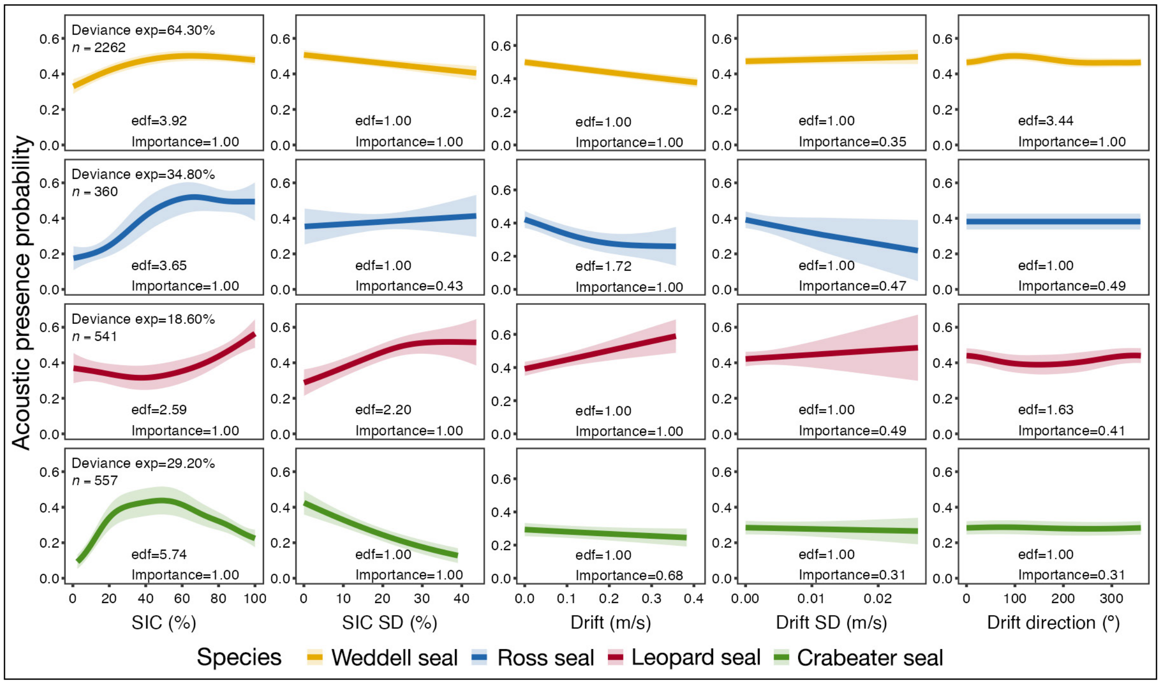

Figure 3. Estimated smooth curves for the effect of sea-ice predictors (SIC, SIC standard deviation, drift, drift standard deviation, and drift direction) on the daily acoustic presence probability of the four pinniped species recorded off PALAOA from 2007 to 2014. Continuous lines and shaded areas represent the mean and two standard errors, respectively. edf = effective degrees of freedom; Deviance exp = explained deviance; Importance = relative strength of evidence.

opportunities. An opposite relationship to SIC variability was detected for crabeater seal (Figure 3), possibly reflecting that this species tends to avoid areas where leopard seals are present or ceases calling when leopard seals are nearby to reduce predation risk (Van Opzeeland *et al*. 2010).

Sea-ice drift drives sea-ice convergence and compaction events (eg Massom *et al*. 2008) and could therefore affect the spatiotemporal variability of fast-ice and pack-ice distribution (Fraser *et al*. 2012), local krill abundance (Meyer *et al*. 2017), the opening/closing of polynyas (sites of open water enclosed by sea ice), and sea-ice cover stability (and therefore its suitability as support, eg for breeding). We found negative relationships between species acoustic presence probabilities and sea-ice drift velocity, except for leopard seal, for which there was a strong positive trend, and no relevant effect of sea-ice drift direction. Negative relationships are to be expected in species known to forage in areas where ocean currents are weak (Wege *et al*. 2021b), which may positively affect krill availability and sea-ice floe stability. Leopard seals, however, breed on the outer fringes of the pack ice, manifesting preference for areas with abundant smaller and thinner free-floating ice floes (Rogers 2009), behaviors that may account for the observed affinity of this species for higher velocity sea-ice drift conditions.

Relationship between sea-ice cover and Antarctic pinniped vocal activity

At SIC levels below 10%, all four pinniped species displayed low acoustic presence probability (Figure 3). Indeed, the lowest relative acoustic activity for each species occurred during the strong negative SIC anomaly that began in early December 2010 and lasted through the 2010–2011 summer (Figure 2). Although the strong negative sea-ice cover anomaly did not seem to affect the onset or presence of breeding-related acoustic activity, it consistently resulted in a threefold average reduction in relative acoustic activity during December 2010–January 2011 across all four pinniped species. These results suggest that ice-dependent pinnipeds may lack the adaptive capacity to adjust their breeding phenology to such rapid fluctuations in sea-ice cover. Strong reductions in or virtual absences of early-summer fast or pack ice could prevent seals from finding optimal ice floes for hauling-out, giving birth, and nursing their pups in traditional breeding areas (Siniff *et al*. 2008). Accordingly, pinnipeds breeding off PALAOA may have been forced to move to an alternative area with better sea-ice conditions during the strong negative sea-ice anomaly in 2010–2011, thereby explaining the decrease in effective acoustic activity off PALAOA. However, the summer of 2010–2011 displayed one of the lowest mean sea-ice extents throughout the eastern part of the Weddell Sea (Figure 1) (Turner *et al*. 2020), likely compromising sea-ice suitability in the larger area off PALAOA as well. Relocating away from traditional whelping areas in response to poor sea-ice conditions has been observed in Arctic ice-breeding pinniped species (Stenson and Hammill 2014). For animals that stayed in the area and bred on the small/

thin ice remnants, high pup mortality rates were reported. Moreover, the energetic cost for pinnipeds to extend/intensify the search for suitable breeding platforms (within or outside traditional breeding areas) is likely substantial, especially given the narrow time window during which reproduction in these species can take place (Van Opzeeland *et al.* 2010) as well as the potential intensification of intra- and interspecific competition for available optimal spaces (LaRue *et al.* 2019). Combined, these factors can take a toll on males' underwater vocal displays and potentially contribute to the reduced acoustic presence probability of true Antarctic pinnipeds off PALAOA.

However, it is still difficult to determine whether sea-ice absence (as breeding platforms), other associated factors (eg prey availability), or a combination thereof triggered the observed reduction in vocal presence in the pinniped species. Rapidly developing technologies that allow for long-term acoustic source tracking and estimation of species abundance based on species-specific calls (eg Barchasz *et al.* 2020) could help to disentangle causality in the relationship between sea-ice conditions and the acoustic behavior of true Antarctic pinnipeds. Improving our understanding of the effects of strong climatic events on Antarctic pinnipeds – and marine mammals in general (eg Schall *et al.* 2021) – is crucial to enable future comprehensive vulnerability assessments in the Southern Ocean. As potential sentinels of ecosystem response to climate vulnerability and change (Hazen *et al.* 2019), marine predators could bridge the current gap in species-specific baseline data that will be otherwise unrealistic to achieve in time if current climatic trends persist. On the basis of a large tracking dataset of marine predators, Hindell *et al.* (2020) identified areas of ecological significance (AES), which included the area off PALAOA. Establishing networks of protection that encompass AESs could therefore represent one potential path toward long-term mitigation of the growing pressures (overfishing, tourism, climate change) experienced by Southern Ocean ecosystems.

Conclusion

To the best of our knowledge, this is the first study in which long-term acoustic dynamics of true Antarctic pinniped species were directly linked to fluctuations in sea-ice conditions. We demonstrated that long-term PAM, together with practical and generalized classification models, can contribute to the long-term and high-resolution baseline of species' breeding behavior, habitat use, and community structure in Antarctica. Even while still within the boundaries of natural/intrinsic variability, strong local fluctuations in the Antarctic sea-ice cover could provide valuable insight into the short-term consequences of rapid key changes in marine ecosystems. In light of the findings presented here, and in the context of current warming trends, it is critically important to better understand how strong fluctuations in sea-ice cover within high-fidelity breeding areas affect the abundance and distribution of key Antarctic predators.

Acknowledgements

O Boebel, S Spiesecke, and L Kindermann; H Klinck, S Riedel, D Steinhage, A Ziffer, and the overwintering teams (Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, Germany); H Schubert (Reederei F Laeisz GmbH, Rostock, Germany); and R Verhoeven, J Hoffmann, and C Müller (FIELAX Services for Marine Science and Technology mbH, Bremerhaven, Germany) all played crucial roles in establishing and/or maintaining the Perennial Acoustic Observatory in the Antarctic Ocean (PALAOA). Partial funding for the PALAOA project was provided by the Bremerhavener Gesellschaft für Innovationsförderung und Stadtentwicklung (BIS). Sea-ice data were provided by the University of Bremen. Open Access funding enabled and organized by Projekt DEAL.

Data Availability Statement

All PALAOA data are deposited at PANGAEA (www.pangaea.de), at: doi.pangaea.de/10.1594/PANGAEA.773610; doi.pangaea.de/10.1594/PANGAEA.845083; and doi.pangaea.de/10.1594/PANGAEA.844106.

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Supporting Information

Additional, web-only material may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/fee.2622/suppinfo