

ECOLOGY

Insights from the first global population estimate of Weddell seals in Antarctica

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The Weddell seal is one of the best-studied marine mammals in the world, owing to a multidecadal demographic effort in the southernmost part of its range. Despite their occurrence around the Antarctic coastline, we know little about larger scale patterns in distribution, population size, or structure. We combined high-resolution satellite imagery from 2011, crowd-sourcing, and habitat modeling to report the first global population estimate for the species and environmental factors that influence its distribution. We estimated ~202,000 (95% confidence interval: 85,345 to 523,140) sub-adult and adult female seals, with proximate ocean depth and fast-ice variables as factors explaining spatial prevalence. Distances to penguin colonies were associated with seal presence, but only emperor penguin population size had a strong negative relationship. The small, estimated population size relative to previous estimates and the seals' nexus with trophic competitors indicates that a community ecology approach is required in efforts to monitor the Southern Ocean ecosystem.

INTRODUCTION

The structure of ocean ecosystems is being rapidly altered around the world because of fishing and climate change, especially as shown by trends in megafaunal species [e.g., (1, 2)], with polar oceans being severely affected [e.g., (3, 4)]. Owing to the remoteness of the Southern Ocean and to the logistical challenges, gathering population data for penguins (Spheniscidae) and seals (Otariidae and Phocidae), which have been proposed as sentinel or indicator species in monitoring programs to assess ecosystem change (5), has long been problematic (6). However, the increased availability of very high resolution (VHR) satellite imagery (~30- to 50-cm spatial resolution) has made documenting a number of species' population changes possible (7, 8), further advancing our ability to detect signals of ecosystem change. Recent examples of VHR applications in the Southern Ocean include assessing Adélie penguin (*Pygoscelis adeliae*; ADPE) and the emperor penguin (*Aptenodytes forsteri*; EMPE) colony populations (9–12), both of which are sensitive to environmental change (13). Little complementary information is available for other Southern Ocean species, although sensitivity to sea ice variability is well researched (13, 14), and thus a holistic understanding of ecosystem structure across the entirety of the Southern Ocean remains elusive. With the advent of VHR imagery, however, we can monitor these key species at appropriate spatial scales, allowing important detection and validation for modeling future (e.g., climate, population) scenarios.

Antarctica's fast-ice habitat is required for reproduction by the Weddell seal (*Leptonychotes weddellii*; WESE), an iconic species that, arguably, is an indicator in key regions of the Southern Ocean

for both sea ice fluctuations and shifts in food web structure due to commercial fishing for Antarctic toothfish [*Dissostichus mawsoni*; (15–18)]. The study of WESE populations in the Southern Ocean presents many logistical challenges. The natural history, demography, physiology, and foraging behavior of the WESE, however, has been intensively investigated since the 1960s, particularly in the vicinity of Erebus Bay, Ross Sea, thanks to its proximity to the largest research base in Antarctica, McMurdo Station. These studies make this species probably the most completely known pinniped anywhere worldwide [including (18–21)]. Until recently, an assessment of the WESE population at regional and global scales has not been possible. The Antarctic Pack Ice Seals (APIS) program, an international collaboration, conducted the largest effort to date using both shipboard and aerial surveys across several years while also building on earlier efforts (22–25). However, a truly concurrent assessment of WESE occurrence in particular at multiple spatial scales has now been made possible through the availability of VHR imagery, an application made feasible by WESE's large size (3 to 4 m in length), dark color against the white sea ice, and propensity to not clump closely like other pinnipeds (26). Moreover, the Erebus Bay research effort has provided key ground validation data for the development and assessment of a satellite-based approach (26, 27), which upon extension to the entire continent allows quantification of the global distribution of this species, along with the physical and biological variables that best explain prevalence at multiple spatial scales.

Following our regional VHR- and crowd-sourced assessment of WESE prevalence and habitat use in the Ross Sea, where the well-known Erebus Bay breeding population exists (28), we now report the first global estimate for this species. We also report on environmental factors that describe seal presence during pup-rearing (i.e., in fast-ice habitat) at regional and continental scales and highlight the utility of our method to detect and monitor population change. These results will facilitate attempts to separate fisheries impacts from climate influences thus to better address conservation goals for the Southern Ocean (4, 6, 29). The WESE is vulnerable to impacts because of climate change and fisheries (18, 30, 31), and the spatially-explicit estimate presented here can provide the baseline against which any future population changes can be identified, as well as

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comparisons with archived imagery (15, 17). By documenting the magnitude, location, and other factors associated with the seals' presence, we will be better able to ascertain reasons behind any future population changes. We discuss the need to periodically compile VHR images to provide updated population estimates on spatial scales not currently available.

RESULTS

A first global population estimate for the WESE

Using satellite images from November 2011 and an established model for converting tallies, i.e., "tags" (features on images of the ice deemed to be a seal) to actual number of WESE (27), we estimated the global population of adult and sub-adult female seals to be unexpectedly low: 202,135 [95% confidence interval (CI): 85,345 to 523,140; Table 1]. This is a corrected estimate of female seals to account for sex-specific haul-out patterns. Our stable age distribution calculations (based on the decadal Erebus Bay demographic study) indicate that for female WESE in the global population, 61% are prebreeders, 4% first-time breeders, 23% experienced breeders, and 12% skip-breeders (Table 1). Considering the four broad regions into which we divided the Antarctic coast, the Ross Sea contained the highest numbers of WESE in Antarctica, representing 41% of the world population (Fig. 1). The Amundsen Sea region contained the smallest proportion of the global WESE population.

Regional and continental habitat characteristics of the WESE

Our best model to describe WESE habitat during pup-rearing [Akaike Information Criterion (AIC) = 2956, df = 2885] included physical variables such as bathymetry (local seafloor slope, depth, and proximity to a submarine canyon), ice conditions (e.g., predictability of fast ice being present during October, at the start of pupping season), and distances to shoreline (Table 2). Biological variables important for WESE presence included proximity to both ADPE and EMPE colonies and size of the nearby EMPE colony. Size of the nearby ADPE colony, providing one existed in the region, did not affect seal presence in this Antarctic-wide analysis. Below, we describe the effects of each variable first, and then we discuss the relationships across the Antarctic regions.

Continent-wide, WESE during pup-rearing were much more likely to be found hauled out in proximity to the shoreline, due to the location of tidal cracks for exit/entrance to the ocean (slope = 3.447, coefficient = 3.447, $z = 6.773$, $P < 0.0001$), with an optimal distance of 1 to 2 km (quadratic effect, coefficient = -0.257 , $z = -7.909$, $P < 0.0001$; Table 2). The effect of the bathymetry variable was strongly positive as well (coefficient = 0.261, $z = 3.119$, $P = 0.002$). Because we transformed bathymetry values by -1 times the natural logarithm of depth, the result indicates that the WESEs' probability of presence decreases as depth increases. This result indicates preference for sufficiently deep areas near shore, where there are predictable tide cracks in the fast ice. Having accounted for ice conditions, proximity to EMPE colonies had a strong negative relationship with WESE presence (coefficient = -12.371 , $z = -7.804$, $P < 0.0001$), as did population size of the nearest EMPE colony (coefficient = -0.14 , $z = -2.956$, $P = 0.003$; Fig. 2). Seals were more likely to be found near EMPE colonies, but the larger the EMPE colony, the less likely seals would be present. In contrast, although the size of nearest ADPE colony was not related to seal presence (coefficient = -0.024 , $z = -0.503$, $P > 0.6$), proximity had a complex relationship with seals: The probability of seal presence was highest around 3 km away from an ADPE colony (linear coefficient = 2.721, $z = 2.806$, $P = 0.005$; quadratic effect coefficient = -0.166 , $z = -3.156$, $P = 0.002$; Fig. 3).

We found regional metrics that helped explain variation in WESE presence (Table 2). Specifically, conditions of the fast ice varied by region, with the predictability of October fast ice during the previous 5 years having a weak positive relationship with seal presence in East Antarctica (coefficient = 0.206, $z = 2.404$, $P = 0.016$) and a strong, negative relationship in the Ross Sea (our reference region; coefficient = 0.289, $z = -3.562$, $P < 0.001$). Note that East Antarctica is several latitude degrees farther north (hence different climate) than much of the Ross Sea. Proximity to coastal glaciers had a strong, negative relationship with seal presence only in the Ross Sea (coefficient = -1.145 , $z = -4.645$, $P < 0.0001$) but was positive in all other regions (Table 2). In the Ross Sea, where the coastal ocean is deep, seals were more likely to be found closer to waters >300 m deep (coefficient = -2.338 , $z = -3.218$, $P = 0.002$). We did not find differences in regional relationships related to abundance of ADPE

Table 1. Population size of WESE by region in Antarctica. Global population estimates for reproductive WESEs on fast ice during November 2011, including the lower and upper 95% confidence intervals, the percent total each region represents of the global population, and stable age distribution for each estimate by region (PB, prebreeders; FB, first-time breeders; EB, experienced breeders; SB, skip-breeders). The regions reported here represent the six, roughly equal-sized areas for crowd-sourcing campaigns conducted via Tomnod [now GeoHIVE; i.e., the approximately 0.55% of fast ice where seals were found (39), including Amundsen Sea (AMU), East Antarctica 1 (EA1), East Antarctica 2 (EA2), Queen Maud Land (QMA), Ross Sea Sector (RSS), and the Weddell Sea and southern part of the Antarctic Peninsula (AP-EAP)].

	Region	Lower	Estimate	Upper	% Total by region	# PB	# FB	# EB	# SB
1	AMU	4,926	9,375	24,373	5	5,719	375	2,156	1125
2	EA1	10,405	23,959	61,801	12	14,615	958	5,511	2,875
3	EA2	10,975	21,862	54,886	11	13,336	874	5,028	2,623
4	QMA	14,038	30,325	75,791	15	18,498	1,213	6,975	3,639
5	RSS	31,415	84,174	223,437	41	51,346	3,367	19,360	10,101
6	AP-EAP	13,586	32,440	82,853	16	19,789	1,298	7,461	3,893
	Total	85,346	202,135	523,141	100	123,302	8,085	46,491	24,256

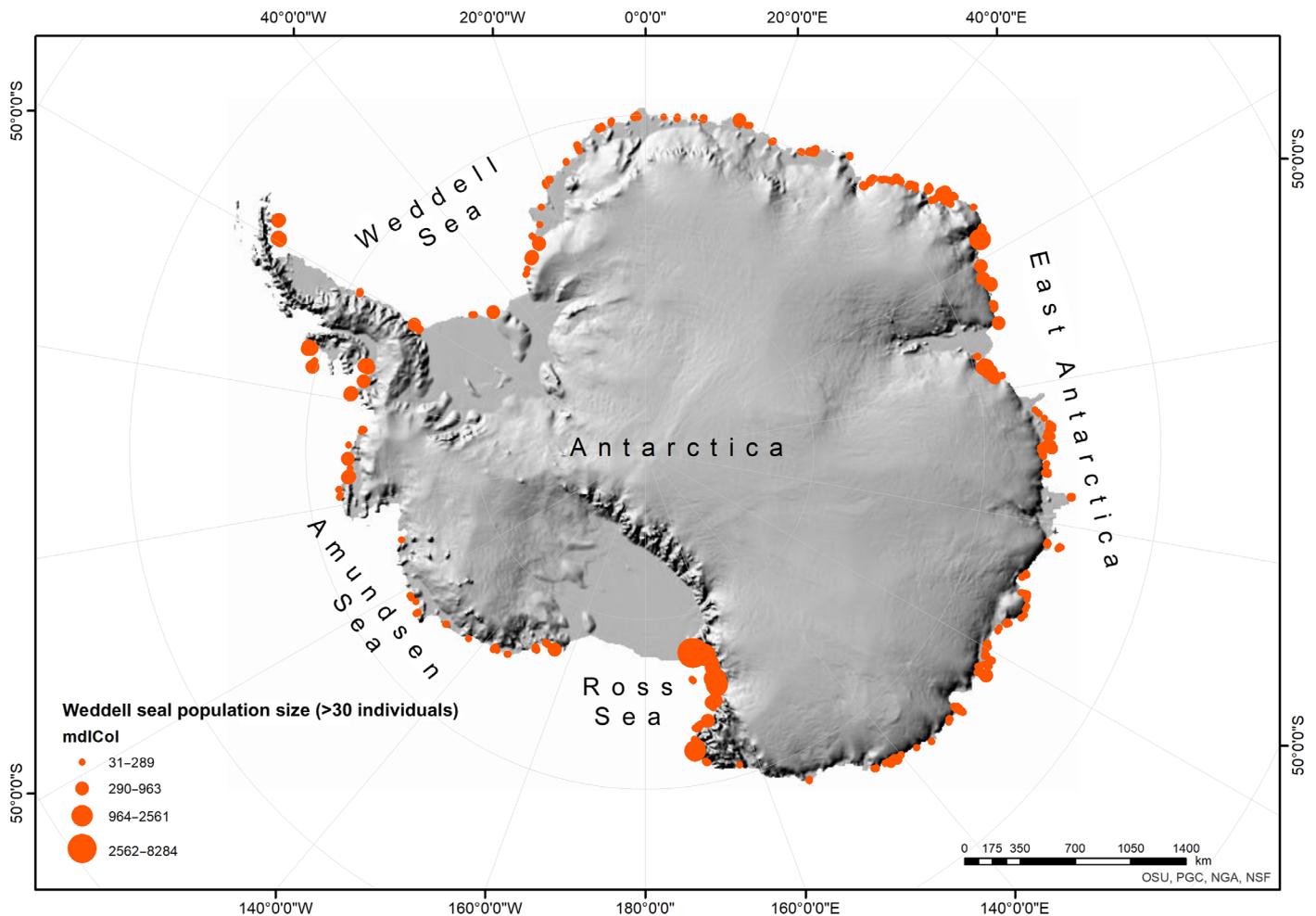


Fig. 1. A map of WESE populations around Antarctica during November 2011. Map of WESE abundance (females only) on fast ice around Antarctica during November 2011 (excluding the northern portion of the western Antarctic Peninsula, where fast ice has disappeared or is decreasing), estimated through a combination of VHR images and crowd-sourcing counts of seals. Numbers of animals across tagging campaigns are referenced in Table 1, including the estimated stable age distribution, based on ground validation from Erebus Bay, Antarctica [e.g., (20)]. The underlying image is the Reference Elevation Model of Antarctica provided by the Polar Geospatial Center in collaboration with Ohio State University, the National Geospatial Intelligence Agency, and the National Science Foundation.

(Table 2). Model goodness-of-fit results show the accuracy of our model to be 0.7568, with specificity = 0.7643 and sensitivity = 0.7492 ($Kappa = 0.5135$). Likelihood ratio tests to evaluate interactions within models (across 11 total candidate models; for example, interactions between region and fast-ice ratio) indicated that the best model (presented above) was a significantly better fit than all other candidate models ($P < 0.05$; Table 3).

DISCUSSION

The first global estimate of the species

To our knowledge, this study provides the first direct population estimate (e.g., counts of individuals) for the global distribution of any wide-ranging, wild animal species on Earth. Prior similar approaches have made approximations from indirect evidence [e.g., guano footprints (9, 11, 12)] or by sampling smaller areas (32–36). Here, we were able to survey all available fast-ice habitats for WESE within approximately 1 month (the pup-rearing month, November) in a

single year (2011)—the spatial coverage of our survey effort has never before been possible, especially across such a large area encompassing the entirety of a species distribution. Given the EMPE is another fast ice-obligate species deemed to be vulnerable to sea ice fluctuations (13) and is likely critically sensitive to future climate change (5), then WESE is in the same predicament on the basis of our VHR-derived estimate of ~200,000 sub-adult and adult female WESE during 2011. Our work indicates that WESEs are not as numerous as previously thought, e.g., ~30% of previous estimates (~800,000 animals) reported from extrapolations of regional counts notably, however, in pack ice (37) (rather than fast-ice habitat, which is breeding habitat and the habitat reported here). The ~200,000 female WESEs accounts for regional differences in actual numbers and thus can be considered a robust baseline for the species. Our estimate here should not be interpreted as evidence for a decrease, or any change at all, in the global population of WESE. Similar to first ever, although indirect estimates for both high-latitude, pagophilic Antarctic penguins, we simply know more than we did previously because satellite images

Table 2. Results of habitat modeling for WESE. Results of the best logistic regression model to describe WESE presence on >260,000 km² of Antarctic fast ice during November 2011 (df = 2885.000, AIC = 2956.328, residual deviance = 2878.328).

	Variable	Coefficient	SE	z_value	Prob_t
1	(Intercept)	91.625	14.321	6.386	0.000
2	scaledmeanslope	0.337	0.154	2.199	0.028
3	l(scaledmeanslope^2)	-0.079	0.035	-2.278	0.023
4	logmeanbathy	0.261	0.083	3.119	0.002
5	adpepresentno	-17.469	4.071	-4.291	0.000
6	logadpedist	2.721	0.973	2.806	0.005
7	empepresentno	11.751	3.637	3.174	0.002
8	logempedist	-12.317	1.571	-7.804	0.000
9	l(logempedist^2)	0.559	0.075	7.463	0.000
10	l(logadpedist^2)	-0.166	0.053	-3.156	0.002
11	logEMPEabund	-0.14	0.047	-2.956	0.003
12	logADPEabund	-0.024	0.047	-0.503	0.615
13	RegionA-B-WAP	-44.96	10.77	-4.176	0.000
14	RegionEAnt	-38.456	10.593	-3.629	0.000
15	RegionWedd_Sea	-44.122	10.695	-4.13	0.000
16	PredictabilityOct5Years	-0.289	0.081	-3.562	0.000
17	logdistToShore	3.447	0.51	6.773	0.000
18	l(logdistToShore^2)	-0.257	0.032	-7.909	0.000
19	logcont300dist	-2.338	0.726	-3.218	0.001
20	lnCanyon	-2.068	0.674	-3.069	0.002
21	fastIceRatio	0.89	0.635	1.397	0.162
22	logglacierdist	-1.145	0.245	-4.645	0.000
23	adpepresentno:logadpedist	1.654	0.371	4.453	0.000
24	empepresentno:logempedist	-1.071	0.305	-3.453	0.001
25	logADPEabund:RegionA-B-WAP	-0.162	0.089	-1.817	0.069
26	logADPEabund:RegionEAnt	0.095	0.04	2.416	0.016
27	logADPEabund:RegionWedd_Sea	-0.021	0.068	-0.328	0.743
28	RegionA-B-WAP:PredictabilityOct5Years	-0.208	0.132	-1.581	0.114
29	RegionEAnt:PredictabilityOct5Years	0.206	0.086	2.404	0.016
30	RegionWedd_Sea:PredictabilityOct5Years	-0.105	0.111	-0.952	0.341
31	RegionA-B-WAP:logcont300dist	2.256	0.728	3.094	0.002
32	RegionEAnt:logcont300dist	2.176	0.728	2.987	0.003
33	RegionWedd_Sea:logcont300dist	2.326	0.731	3.181	0.001
34	RegionA-B-WAP:fastIceRatio	-2.029	0.787	-2.581	0.01
35	RegionEAnt:fastIceRatio	-0.526	0.688	-0.758	0.448
36	RegionWedd_Sea:fastIceRatio	-1.442	0.738	-1.951	0.051
37	RegionA-B-WAP:logglacierdist	1.492	0.317	4.696	0.000
38	RegionEAnt:logglacierdist	0.854	0.254	3.342	0.001
39	RegionWedd_Sea:logglacierdist	1.244	0.286	4.34	0.001

provide unprecedented access to ground conditions (9, 11). Our WESE population estimate is actually in line with results of genetic analysis, conducted using seal tissues collected near Terra Nova Bay, Ross Sea, that indicated the effective WESE population size (N_E) to

be ~150,000 animals (38). Even after considering that the previous population estimate, based on surveys of pack ice, probably included males and our estimate does not, it is very likely that the global WESE abundance is <50% of that original estimate.

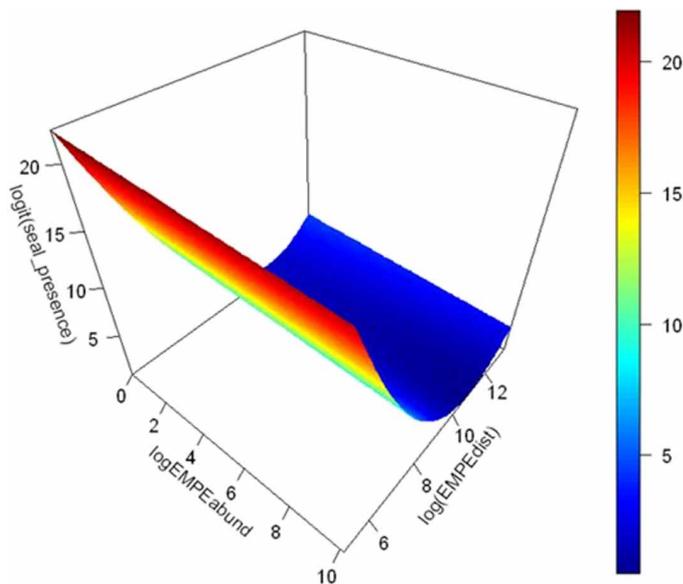


Fig. 2. A two-dimensional partial dependence plot showing the effect of the size of the nearest EMPE colony on the probability of WESE presence on Antarctic fast ice. Two-dimensional partial dependence plot showing the combined effect of EMPE abundance ($\log(\text{EMPEabund})$) and distance to the nearest EMPE colony ($\log(\text{EMPEdist})$) on the probability of presence of WESEs around the fast ice of Antarctica during November 2011. WESEs are more likely to be found close to smaller (<100 breeding pairs) EMPE colonies.

Given that the WESE has been designated an indicator species to assess ecosystem change (6), adding to the need-for-conservation/management pressure is the utility and efficiency by which volunteers from around the world produced the timely results that otherwise would not have been possible. The logistics of completing ground surveys is infeasible because of the remoteness of areas that may contain seal colonies, as discussed in (39), because unlike other Antarctic seals, WESEs are typically found in fast-ice areas away from open water. Ground surveys are only possible in a very small subset of select areas near established research bases (20, 40). Before this study, the largest effort to understand the world population of pack ice seals was the APIS program (24, 25, 41), which took place over the course of several years but covered a small fraction of the area that we surveyed [as discussed in (39)]. With the “power of the crowd” (e.g., >320,000 volunteers) in the course of about 1 year, we searched inaccessible fast-ice areas, reduced the search area for seal presence (39), estimated the population size, made comparisons with environmental factors, and confirmed a continent-wide, interactive relationship among sympatric, and trophically competing marine mesopredators [i.e., the penguins and seals; (17, 42)]. This work can be added to the list of population assessments that have been conducted in Antarctica using VHR imagery [EMPE: (9, 43); ADPE: (11); see summary in (44); and chinstrap penguins (*Pygoscelis antarctica*); (12)]. Furthermore, our remote sensing approach provides a safe and noninvasive method of gaining precise population data and can be done on a routine basis. If predictions of change in the Southern Ocean over the next 100 years correctly forecast warming sea surface and air temperatures, altered winds and sea surface salinity, ice shelf loss, and increases in invasive species among others (45, 46), then large-scale approaches such as ours to monitor the Antarctic ecosystem will be of increasing importance.

Part of the success of our innovative approach to study WESE populations was due to several unique aspects of their life history and because ground validation in Erebus Bay was possible [e.g., (47–50)]. WESE females raise pups on annually predictable fast ice during austral spring (30, 51) and are mixed-capital breeders, meaning they remain visible on the ice for long periods (31, 52) and so do not stray away from their haul-out locations (53, 54) during November. With VHR imagery and owing to the cloudy marine layer dissipating near the coast, very few locations could not be surveyed because of clouds or poor image quality (39). Thus, we were able to collect images during a short time when WESE presence was most stable (low level of foraging, males attracted to females who, in turn, were attached to their pups) and were able to verify our VHR- and crowd-derived estimates (27), thus making this research possible and otherwise far more precise.

Although we have suggested that our estimate from 2011 is a first baseline, it is important to note that in reviewing historic records from aerial and ice-based surveys in the Ross Sea, there does appear to have been a downward shift in seal numbers in that region [cf. (51, 55)]. Recently, despite no change in sea ice extent nor duration between Edisto Inlet (northern Victoria Land and near the shelf break) and southern McMurdo Sound (as far south as possible, in southern Victoria Land), over the course of ~50 years, the number of seals in the northern area, known as a seal hotspot, apparently has dropped markedly (16). In November 1967, >100 were counted in the inlet and surrounding bay (51), but in November 2010, there were <10 (16); and an additional aerial survey on 31 October 2018 found only 4 in that location (M.L. and L.S., personal observations). Moreover, as first judged in the 1960s, >2500 WESEs hauled out on the fast ice in extreme southern McMurdo Sound to molt (following the pupping season), an aggregation thought to result from temporary movement of northern Victoria Land seals (56), but in recent years, numbers of these possible WESE immigrants from the north has decreased by an order of magnitude to <200 (18). The southern movement of seals for purposes of the molt, during which they do not feed, is the consequence of fast ice disappearing in the north by January, not so in the south (56). Therefore, it does appear that there has been a major reduction in WESE numbers in Victoria Land during the past few decades, and we suggest that our estimate here of ~84,000 female WESE in 2011 is possibly fewer than was present in the early 1960s when research in the Ross Sea began. These reductions are despite the WESE breeding population in Erebus Bay (central southern McMurdo Sound) increasing over the past 20 years (16, 18) and likely being the largest breeding concentration of this species in the world.

Habitat suitability for WESEs

We also report the physical and biological factors that influence the southernmost breeding mammal in the world over the entirety of its range [with exception of the west coast of the northern Antarctic Peninsula and islands of the Scotia Sea, where the species' numbers are small and have decreased because of disappearance of the historically minimal fast ice there (30)]. Replicating methods and hypotheses laid out previously for our Ross Sea assessment (28), we found that with respect to ice and ocean depth, WESE elsewhere around the continent are using habitats similar to those used in the Ross Sea (Table 3). Proximity to both the continental shore and deep waters remained important explanatory variables in our circum-polar analysis. As suggested (28), deep waters are a proxy for prey

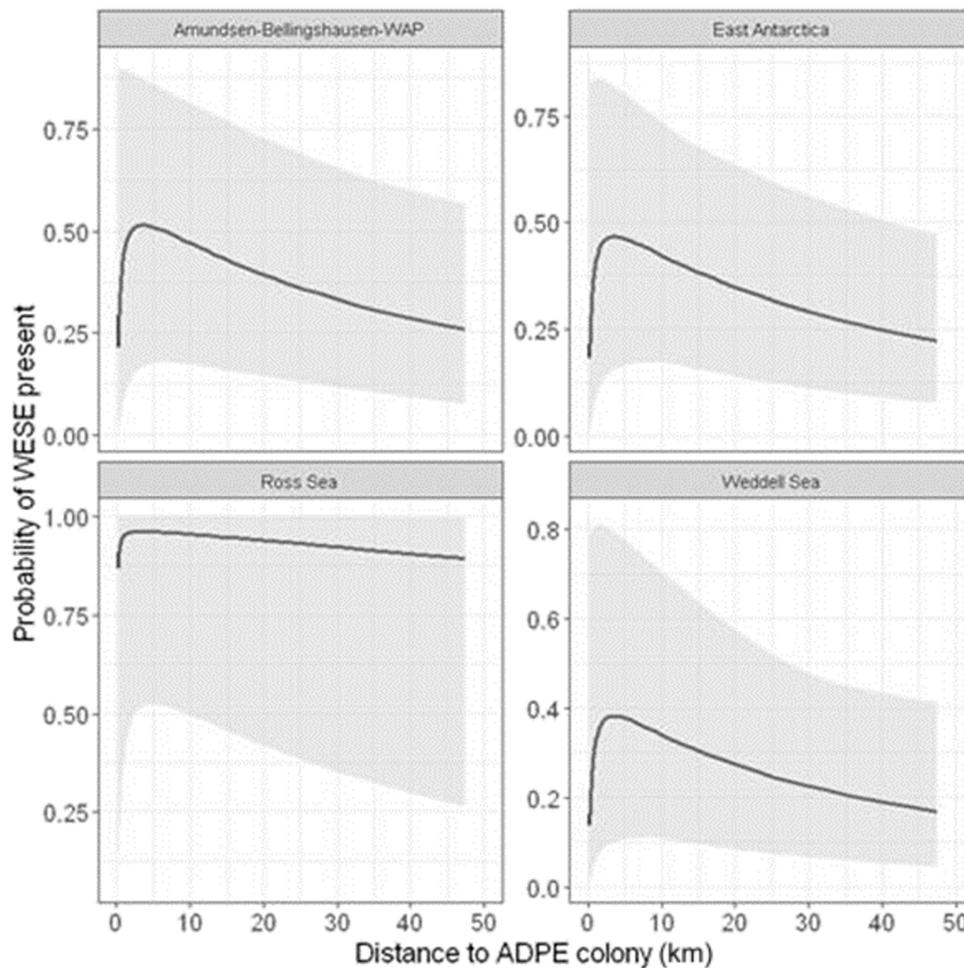


Fig. 3. A partial dependence plot showing the effect of ADPEs on the probability of WESE presence on Antarctic fast ice. Partial dependence plot showing the effect of ADPE distance on the probability of WESE presence around Antarctic fast ice during November 2011 for each of the four oceanographic regions defined in this paper. Regions ($n = 4$) are defined in Fig. 4.

Table 3. Results of the likelihood ratio tests to compare 10 candidate models to our top model. We systematically removed one variable or one interaction from our top model: 1) October ice predictability over 5 years; 2) regional effect of October ice predictability over 5 years; 3) distance to ocean depth of 300 m; 4) regional effect of distance to ocean depth of 300 m; 5) fast-ice ratio, calculated as the ratio of the distance from seal location to ice edge divided by distance from shore to ice edge; 6) regional effect of fast-ice ratio; 7) distance to nearest glacier; 8) regional effect of distance to nearest glacier; 9) ADPE abundance; and 10) regional effect of ADPE abundance. Regions ($n = 4$) are defined in Fig. 4.

	Model	Mean_prChisq	Median_prChisq	Max_prChisq	% Significant
1	No_Oct5Yrs	0.0000	0.0000	0.0000	100
2	Region_Oct5Yrs	0.0000	0.0000	0.0004	100
3	No_Dist300m	0.0000	0.0000	0.0001	100
4	Region_Dist300	0.0003	0.0001	0.0060	100
5	No_FastIceRatio	0.0645	0.0168	0.6805	73
6	Region_FastIceRatio	0.0442	0.0081	0.5159	80
7	No_GlacierDist	0.0000	0.0000	0.0004	100
8	Region_GlacierDist	0.0001	0.0000	0.0020	100
9	NoADPEabund	0.0041	0.0003	0.1676	98
10	Region_ADPEabund	0.0042	0.0003	0.2325	99

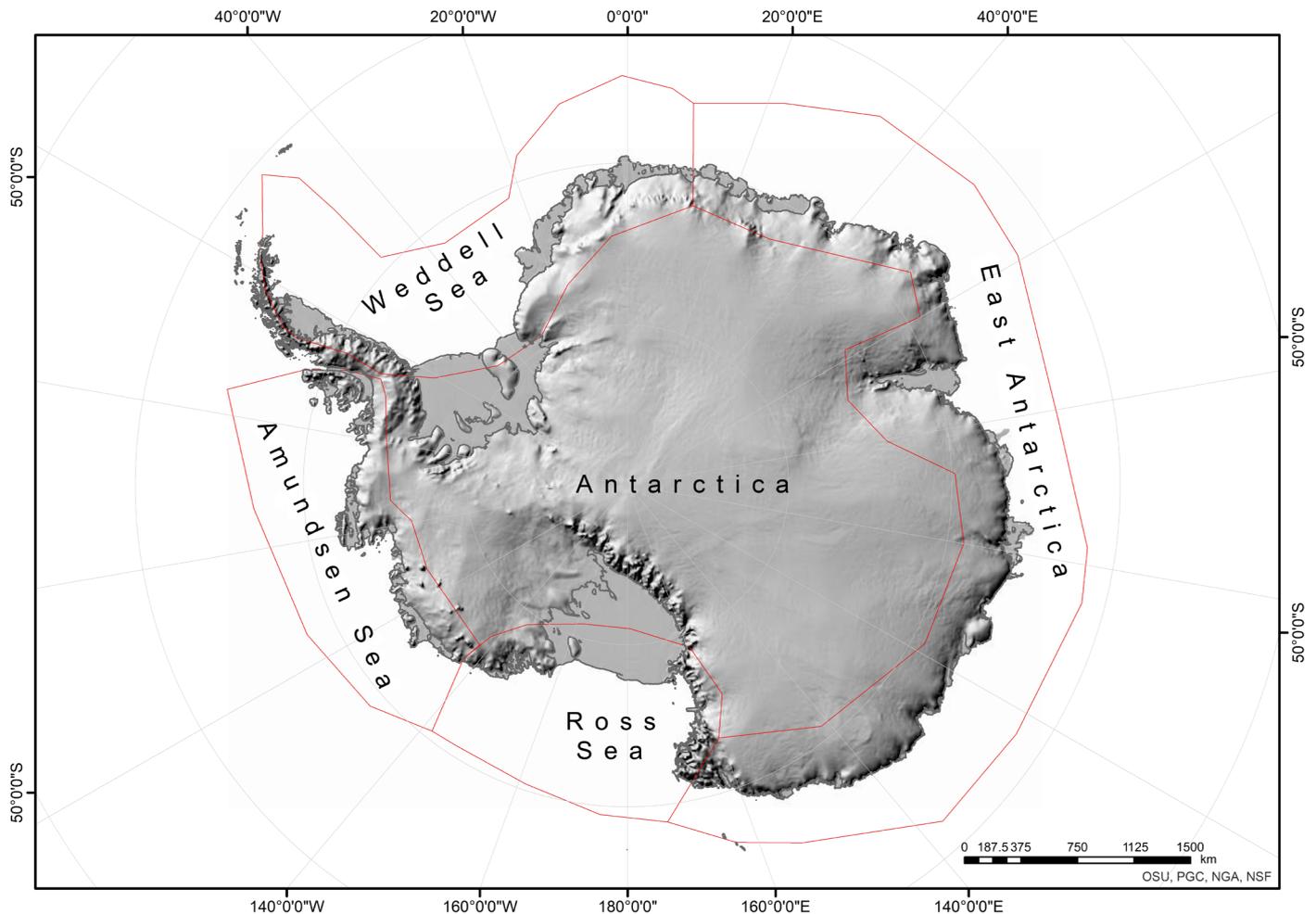


Fig. 4. Regional boundaries for modeling WESE presence in Antarctica. Four regions around Antarctica outlined in red for habitat modeling of WESEs around the continent, with exception of the northern part of the western Antarctic Peninsula. We defined regions irrespective of animal presence and considered regions exclusively based on oceanographic features such as currents, gyres, bathymetry, and general pack ice dynamics.

availability (greater volume to hold more fish), and proximity to the coastline is associated with regularly occurring tidal cracks, allowing exit/entrance to the ocean during the pupping season (57).

Another key finding, however, is the regional distribution of fast ice playing a significant role in determining seal presence. For example, fast-ice conditions in the Ross Sea, which was found by our study to be more favorable and more available than elsewhere, including in the Weddell Sea, may be one reason why this region is so densely populated with WESE. In the Ross Sea, the fast-ice extent (width) is adequate enough to allow the seals to be far away from the fast-ice edge, thus safe from predators [e.g., killer whales (*Orcinus orca*) (58, 59)], as well as being stable and predictable. Ross Sea fast ice, therefore, can be understood as a climate refugium for both pupping and molting WESEs, as it has throughout the Holocene (60). In addition, the Ross Sea is incredibly productive, with a robust, diatom-based food web occurring in the marginal ice zone of the Ross Sea polynya (and three smaller polynyas), the largest coastal polynya in the Southern Ocean (61, 62). The high numbers of ADPE and EMPE in the Ross Sea may also reflect the high productivity of this area, contributing ~35 and ~25%, respectively, to

their total global populations (9, 11, 63). The relative contribution of Ross Sea WESE to global numbers (~40%) is thus on par with the penguins.

Interspecific competition between seals and penguins

Perhaps most interestingly and unexpectedly [save for our earlier findings (28)], we found further support to suggest that spatial patterns of WESE presence are associated with the proximity to colonies of the two high-latitude, sea ice-obligate penguin species. In slight contrast to what we found in the Ross Sea (28), at the continental scale (and taking into account four different physiographic/oceanographic regions), the relationship is such that WESEs are most likely to be present at a distance of 3 km from the nearest ADPE colony, regardless of colony size. On the other hand, in the Ross Sea, both the size of, and distance from, nearby ADPE colonies were associated with WESE presence. That is somewhat understandable as in the Ross Sea sizes of ADPE, colonies vary from some of the smallest to the near-largest for the species (11, 64). When broken down by region, only East Antarctica came close to having a significant impact regarding ADPE colony size ($P < 0.052$). However, the East

Antarctic region is the largest of all of our defined regions (Fig. 4), and, more importantly, the sizes of ADPE colonies are smaller and less variable than they are in the Ross Sea—only one of 33 colonies in East Antarctica exceeds 50,000 pairs (11, 44). In the Ross Sea, there are three colonies >200,000 pairs (as of 2011), and four others >70,000 pairs, with the larger size found in only one other location [eastern tip of Antarctic Peninsula; (44, 64)]. Furthermore, the ADPE colonies of Victoria Land have doubled in size since the year ~2000, including Cape Hallett, on the shores of Moubray Bay/Edisto Inlet just to the south (40 k increasing to 70 k pairs). Not far to the north of Moubray Bay, ADPE colonies have also increased markedly, e.g., Cape Adare from 250 k to 340 k pair, with other large colonies nearby (11, 64). Those are the Victoria Land locations, where decreases in numbers of WESE have been noted [see above (16)]. Because of their sheer numbers (millions of penguins versus thousands of seals), are ADPE colonies outcompeting seals for food in these areas, as both depend greatly on Antarctic silverfish (*Pleuragramma antarcticum*) in their diets (18)? Understanding the community structure of marine predators is a critical aspect of monitoring for the Ross Sea Region Marine Protected Area in which the WESE has been proposed as an indicator species (6) and indeed for comprehending marine ecology in general. Our findings provide a first regional capacity to do this.

Regarding EMPE, the extremely even spacing of colonies (44) indicates intraspecific competition for food, as between colonies, there is ample fast ice for EMPE requirements. The variance of between-colony distance is very low. The competition that spaces EMPE colonies, for a couple of reasons, may also involve the spacing of WESEs. First, both species are associated with deep water and proximity to cross-shelf, submarine canyons [see above and (44)]. Second, there are many similarities in ecological aspects of the annual cycles and life histories of the WESE and EMPE, including the importance of silverfish in the diet, equivalent diving capabilities (depth), and phenology of pup weaning and chick fledging [i.e., an important time for maximized prey availability (42)]. The fact that WESEs are negatively related to EMPE colony size in the immediate vicinity supports the evidence for interspecific competition. In somewhat of an experiment, the six newly detected EMPE colonies (43) were found within the gaps between large WESE breeding aggregations. It might pay to look for additional EMPE colonies within other gaps in the circumpolar distribution of WESE as determined by this study (Fig. 1).

Last, we acknowledge that, with respect to distances/depths that we report being associated with higher presence of WESE in our most-supported model, our horizontal precision is 5 km (i.e., the presence/absence for WESE around the entirety of the coastline, minus the Western Antarctic Peninsula (WAP), was tiled into 25-km² grid cells). Across >260,000 km² of available fast ice in 2011, cell sizes of 25 km² allowed for a reasonably precise approximation of WESE habitat associations [cell size that is inclusive of >3 haul-out locations within Erebus Bay, indicating even a within-population spatial resolution (56)]. However, in some locations around Antarctica, for instance, Victoria Land, landscape features can change markedly within just 5 km, especially the coastal depth. For example, we found the vast majority of WESE to be within 5 km of shore and specifically 1 to 2 km, but sometimes the centroid of the 5-km grid cell was actually on land. This, then, was partly the reason for this seemingly precise result. Our goal here was not to derive exact measures (depths and distances) of optimal WESE habitat but rather to look

at patterns that emerge to help understand the species' overarching habitat associations over the entirety of its range. So, although we mention higher WESE presence at "optimal" distances from certain features (shoreline, depths, and penguin colonies), the larger patterns we wished to focus on indicated that WESE are more likely to be present near to shore, in the vicinity of (small) EMPE colonies, and close to deep waters. In the case of ADPE, this proximity seems to indicate that their locations may be driven by the presence of resources that both species share (food or capes/islands that hold fast ice in place). Too close a distance may indicate too much competition, and farther away may mean being farther from resources. Moreover, because ADPE colonies tend to occur in clusters (44), getting farther away from one colony may mean getting closer to another. Therefore, if indeed competition between these two mesopredators for resources determines their place along the coast, then the location of WESE colonies is driven by the location of ADPE colonies within the cluster, in addition to the complex interplay of the factors evaluated here (distance to shore, water depth, reliability of fast ice, etc.). Additional work on WESE distribution within ADPE colony clusters might reveal insights into understanding the ecology of both species. Future efforts could include understanding the habitat drivers of WESE abundance or changes in abundance over time. This work is beyond the scope here.

In summary, our study indicates a smaller global population size of WESE (~200,000 female seals) than most other previously published estimates, with the difference being due to overcoming logistical constraints of working in the high-latitude sea ice zone and not due to a decrease in population size. Rather, our estimate is consistent with one other estimate that was genetically derived (38). We also identified key habitat variables, both physical and biological, that influence the regional distribution of WESE during the spring breeding season. Proximities to both the continent and deep waters are key explanatory variables for all regions, whereas fast-ice conditions are the key variable distinguishing different regions and different population sizes. Also unexpected, WESE are not found everywhere despite the extensive longitudinal prevalence of suitable fast ice. Only 0.55% of suitable fast ice has WESE (39). Last, spatial relationships between the seals and the two high-latitude penguin species highlight the need to further advance the understanding of the coastal Antarctic food web, dominated by Antarctic silverfish. Our approach provides both an important baseline for assessing future changes in WESE distributions and a technique whereby WESE, along with Antarctica's two sea ice-obligate penguin species, can be used as effective indicators of prey availability and other environmental changes. Together, as indicators, they represent the means by which changes in the structure and function of high-latitude, coastal Antarctic ecosystems can be deduced [see also (18, 65)].

MATERIALS AND METHODS

Using counts of WESEs from VHR imagery from November of 2011, we addressed two interconnected objectives: (i) a population estimate of the adult and sub-adult female seals and (ii) the variables that best describe the spatial patterns of WESE presence around Antarctica. We focused on the entire Antarctic coastline [initially >260,000 km²; (39)], specifically the land-fast ice area that rings most of the continent and on which the seals haul out for pupping. We excluded the west coast of the northern Antarctic Peninsula because of the absence of, or disappearing, fast ice (66–69) and because of possibly

misidentifying WESE with sympatric southern elephant seals (*Mirounga leonina*) or Antarctic fur seals (*A. gazella*) (30). Because fast ice in that region is disappearing (30), we reasonably expect a low prevalence of WESE along the west coast of the northern Antarctic Peninsula based on shipboard observations [e.g., (58)].

VHR imagery and community science

We reported results of a “search-area-reduction” survey with the Tomnod platform (now GeoHIVE; Maxar Technologies) to determine the extent of WESE presence in Antarctic coastal habitat (39). Using those data, we focused on locations of probable seal presence to conduct the crowd-sourced tagging campaign that constitutes the basis of the population estimates reported here (i.e., tallying features registered as seals in a VHR image). Briefly, we (27, 39) reported on the required VHR image selection, delineation, and methods that resulted in understanding that WESEs are likely present on only 0.55% of Antarctica’s land-fast ice during spring (November pupping season) 2011. Here, we used the same set of images focusing on one VHR image per sequential location to avoid the potential of double-counting seals and thus to derive a continent-wide estimate under the well-founded assumption that, during the pup-rearing period, seals are highly site specific (53, 70). Although most locations with seal presence were small areas, well within the confines of a single VHR image “footprint” (~255 km²), we buffered these probable seal locations by 500 m to ensure that no seals would be missed in the respective general vicinity. We then effectively “clipped” these buffered areas of probable seal presence from the satellite images such that only the places we wished to have searched were considered for inspection (i.e., no erroneous or extra spaces of fast ice were shown to “the crowd” of volunteer taggers). We then uploaded the imagery to the Tomnod platform organized into six regions described below [see (39) for details] and then launched our online “Satellites Over Seals” tagging campaign.

Relying on our knowledge of the Southern Ocean ecosystem, physiography, bathymetry, oceanography, and seal ecology (28), we hypothesized regional differences in seal abundance and density among four large regions. These regions were East Antarctica (including Queen Maud Land, approximately 0°E to 160°E), the Ross Sea (160°E to 130°W), the Amundsen and Bellingshausen Seas (130°W to 75°W), and the Weddell Sea (60°W to 0°E). However, some of these regions were too large to be loaded into a simultaneous web interface. For example, we could not host all images across the entirety of East Antarctica (an arc of ~160° longitude) at the same time with the same map projection on the web interface. Therefore, we first divided the Antarctic continent into six regions for the crowd-sourced campaign (via Tomnod’s web platform) based on the amount of area that could reasonably be viewed within a single web-based map projection. These regions were derived irrespective of known WESE biology as follows: Amundsen Sea, Antarctic Peninsula (i.e., lower portion of western Antarctic Peninsula plus all the east coast of Antarctic Peninsula; representing the Bellingshausen Sea, on west, and western Weddell Sea, on the east); Queen Maud Land, East Antarctica 1 (~70°E to 94°E); East Antarctica 2 (96°E to 160°E); and the Ross Sea. We provide estimates of seal abundance for these six regions. Once we obtained the counts after completing the campaign, we divided the data into the four abovementioned regions for analytical purposes (Fig. 4). Therefore, these four large ecological regions as defined for our analysis are the only regions through which we attempt to describe regional effects of habitat on WESE presence.

Estimating WESE abundances using volunteer taggers

Our crowd-sourced tagging campaign was promoted via email lists within DigitaGlobe Inc., through social media, and with the help from partnering nonprofit organizations such as Antarctic and Southern Ocean Coalition. We also advertised via the online community science hub SciStarter. A tutorial of how to tag WESEs was included on the front page of the website so that volunteers could see examples of what to tag and what not to tag. After reviewing the tutorial and examples, volunteers were shown a 500-m by 500-m “map” or section of the original satellite image to inspect and tag features they presumed to be seals [see (39) for details]. Details on the tagging campaign, how images were searched and when they were sufficiently searched and retired from further inspection, are described in (27).

To assess and improve the error in counts derived from volunteer tags, as previously detailed (27), we first ranked volunteers on how well they agreed with each other in tagging features and similarly ranked features based on the ranking of surveyors placing tags on them. This algorithm is called “CrowdRank” [see also (28, 39) for details]. We then developed a correction factor by filtering surveyors to include only those that had a CrowdRank of 80% or higher (i.e., those that most agreed with each other) and then comparing surveyors’ tagged estimates to those by an expert. After correcting for surveyor error, we used ground counts from Erebus Bay, Ross Sea, the location of a long-term, intense demographic study [e.g., dozens of publications, somewhat “book-ended” in (47), and (50)] to develop two regression models that account for the proportion of seals not detected in satellite images, and for year, time of day, and sensor effects on seal counts. One of the models, accounting for individual haul-out location effects, resulted in the most accurate and precise estimates. We used this model to predict locations elsewhere around the continent. However, because the model uses individual haul-out location effects, each predicted value must be for one of the nine locations at Erebus Bay. To use this model elsewhere in the continent, at each location, we predicted abundance as if it was each one of the nine reference locations at Erebus Bay. This resulted in nine predicted estimates for the same location. We then averaged all nine estimates, weighted by the relative abundance of seals at each of the Erebus Bay reference locations. Because we also predicted the upper and lower 95% limits of the estimates, once we obtained an estimate of seal abundance and confidence limits for each location, we added these by region, thus obtaining regional estimates and confidence limits, applicable as well continent wide. Full details on the estimation and correction for surveyor bias, the regression models to adjust counts for seals not detected and other important effects, and model evaluation and goodness-of-fit are provided in (27).

Correcting for counts of only sub-adults and adult females

At the time we chose for the satellite images (the month of November), WESE females spend most of the time lying on the fast ice nursing their single, newly born pup, which are too small to be detected on an image (26). We tested for the possibility that the volunteers counted the pups by including a time effect in the regression model to estimate abundances. Specifically, we divided the counts into early and late November and evaluated whether there was a significant difference between these. We found no evidence or any indication that counts increased over time. We are thus confident that the counts, within our time envelope, include only seals 1 year old and older. Here, we refer to any seal that has bred at least once as an

adult, and all others (excepting newborn and preweaned pups) as sub-adults.

Although the sex ratio of WESE at birth is 50:50, there is evidence that the sex ratio becomes more female-biased with age (50). Furthermore, we cannot assume that our volunteers counted all sub-adult and adult seals on ice regardless of sex, because males spend most of their time maintaining underwater territories (71). So, males are more likely to be missed by both the VHR snapshot and by the ground counts used to correct the volunteer estimates. An additional compounding problem in understanding which seals are being counted is that the Erebus Bay locations used for the ground counts are pupping locations, and most seals at these locations are adult females. Sub-adult seals are the predominant age class at locations peripheral to those at Erebus Bay, especially so for sub-adult males (70, 72). Thus, the sex and age ratios of the ground counts at Erebus Bay are not representative of all the locations counted by our volunteers throughout the continent.

To correct for the biased age and reproductive-status composition of the ground counts at Erebus Bay, we first assumed that the larger regional and global populations of female seals would be at a stable age distribution (73). We used data on the probability of survival and probability of reproducing from long-term studies at Erebus Bay (20, 74) to calculate the “expected ground count” at any Erebus Bay location if the location’s population composition was at stable age distribution. Given the expected and observed counts, we calculated an inflation factor for the ground counts so that the age and reproductive status composition would be comparable to that of the regional and global counts: 1.283. To address the differential detectability of males in the counts, we chose to adjust the ground counts so that they excluded males, assuming that the ratio of males to females in any haul-out location is the same as that of the nine Erebus Bay locations where the ground counts were conducted. We then adjust the total estimates for the percent of females in the ground counts by shrinking the ground counts on the basis of the proportion of males found in the ground counts: 0.779 (excluding pups). Therefore, the correction factor to the global and regional estimates to include only adult and sub-adult females (i.e., no pups or males) is $1.283 \times 0.779 = 0.9995$.

Modeling habitat suitability of WESEs

Some locations, owing to some surveyors erroneously tagging features that were presumed seals in some images [e.g., (39) reports high false-positive rates], may be considered seal haul-outs despite no seals actually being present. Conversely, some locations may indeed be seal haul-outs despite no surveyor ever placing a tag on the image. Our correction method addressed these two potential sources of error. After the correction, the locations deemed to have seals and be haul-outs were scored 1 and 0 otherwise. To understand the characteristics that best describe the habitat preferences for WESEs, we replicated methods outlined previously (28) and addressed hypotheses derived from that work. Briefly, we focused our testable hypotheses on a combination of physical and biological characteristics (Table 4) and considered the same 5-km by 5-km grid to organize locations of probable seal presence and absence. Thus, we aggregated the presence/absence data from the 500-m grid cell to the 5-km grid cell. Using the 5-km spatial grid, we log-transformed all distances (measured in meters) and then used the statistical software R (75) to construct logistic regression models to determine the physical and biological characteristics that best described probability of

WESE presence. Our a priori hypotheses and justifications are as follows:

1) Distance to deep water—WESE presence should be associated with shorter distances to waters deeper than 300 m, as such depths included the typical foraging depth range of WESEs (28, 76–79) and should act as a proxy for larger volume of prey availability. In other words, the seals may not live in a grid cell containing waters >300 m deep but perhaps in close proximity to it, which is what differentiates this hypothesis from hypothesis no. 3 below.

2) Seafloor slope—WESE females need to regain mass quickly after weaning their pups, so we hypothesized that they will select haul-out locations in proximity to favorable foraging areas, i.e., areas where the seafloor has a steeper slope (80), likely representing areas where currents and thus nutrient flux are stronger and, in turn, accounting for increased benthic community (and prey) richness (81).

3) Mean seafloor depth—Grid cells with seal presence should be associated with relatively deep water (76–80).

4) Ratio of fast-ice width—WESE presence will be low in areas of narrower fast ice thus putting them closer to ice edge, as well as where broad fast-ice places them far away from open water (i.e., where the ice edge is tens of kilometers distant from the coast). Presence will be higher at middle distances from the ice edge and areas with moderate fast-ice width (28).

5) Distance to shore (land or islands)—WESEs are more likely present near the shoreline, where there is a higher likelihood of tidal cracks (28) that allow access to the water.

6) Distance to glaciers—In addition to the persistent cracks related to no. 5, pressure on the fast ice caused by moving glaciers can cause cracks in the fast ice that also provide seals with access to the water (23).

7) Predictability of fast-ice cover—WESE presence will be correlated with areas having higher probability, year-over-year, of fast-ice presence during pupping (30).

8) Proximity to a subsea canyon—Differentiating from the slope hypothesis (no. 2), grid cells with WESE presence should specifically be associated with continental shelf canyons, allowing proximity of greater volumes of water within which to forage.

9) Distance to ADPE colonies—Given that these penguins and the seals share some of the same prey in a competitive relationship (18), seal abundance is positively correlated with distance from the nearest ADPE colony (28), i.e., seal abundance is low in areas close to ADPE colonies. The relationship is asymptotic such that ADPE abundance effects disappear after some distance and is modulated by the size of the nearest colony [see (44) for distribution of ADPE colonies by size].

10) Size of nearest ADPE colony—Seal abundance is inversely correlated with size of the nearest ADPE colony (28), i.e., seal abundance is low in vicinity of large ADPE colonies (44), with relationship modulated by the distance to the colony.

11) Distance to EMPE colonies—Seal abundance is positively correlated with distance to the nearest EMPE colony (28, 44). The expectation is the same as with hypothesis no. 9.

12) Size of nearest EMPE colony—WESE abundance is inversely correlated with size of the nearby EMPE colony (28), i.e., few seals occur near to a large EMPE colony (44). The expectation is the same as with hypothesis no. 10.

13) On the basis of results in (28), we hypothesized a regional effect on WESE presence, i.e., one that would be dependent on varying oceanographic, physical, and biological attributes in the four Antarctic regions we defined (Fig. 4).

Table 4. Habitat definitions for hypothesis testing to determine the variables that best describe the probability of WESE presence around Antarctica during November 2011. All distances and depths were calculated in meters from the center of the grid cell and in accordance with the spatial projection (Antarctic Polar Stereographic), but note that for practical reasons, we discuss horizontal distances in kilometers.

Covariate type		Covariate	Definition
Numeric	1	LGDI_DEEP	Ln(distance to <300 m bathymetric contours, m)
Numeric	2	SLOPE	Scaled mean bathymetric slope (m) within grid cell
Numeric	3	MEANBATH	Mean bathymetric depth (m) within grid cell
Numeric	4	LGDI_800m	Ln(distance to continental shelf break)
Numeric	5	ICEWIDTH	Ln(Perpendicular distance from edge of continent to edge of fast ice)
Numeric	6	LG_ICERATIO	Ln(ratio of distance to edge/ice width)
Numeric	7	LGDI_SHORE	Ln(distance to shoreline)
Numeric	8	LGDI_GLAC	Ln(distance to coastal glacier/ice tongue)
Numeric	9	LGDI_ICEEDGE	Ln(distance to nearest ice edge)
Numeric	10	PERSIST2YRS	Persistence of fast ice over past 2 years
Numeric	11	PERSIST3YRS	Persistence of fast ice over past 3 years
Numeric	12	PREDOCT5	Predictability of fast ice in December over past 5 years (0–5)
Numeric	13	PREDECS	Predictability of fast ice in October over past 5 years (0–5)
Factor	14	DECICEPRES	Binary presence (0/1) of ice in December 2011
Factor	15	INCANYON	Binary presence of grid being within a bathymetric canyon
Factor	16	INTROUGH	Binary presence of grid being within a bathymetric trough
Factor	17	REGION	Reference region is the Ross Sea
Factor	18	ADPEPRES	Binary presence of ADPE in the grid
Numeric	19	LGEMPEABUND	Ln(size of nearest EMPE colony (breeding pairs))
Numeric	20	LGADPEABUND	Ln(size of nearest ADPE colony (breeding pairs))
Numeric	21	LOGEMPEDIST	Ln(distance to nearest EMPE colony (m))
Numeric	22	LOGADPEDIST	Ln(distance to nearest ADPE colony (m))

Because the grid cells in which WESE were detected represent only 0.55% of available fast ice (39), there are far more grid cells of fast ice without seals than with seals (some of these “empty” cells have EMPE colonies). Seals were present in 1684 grid cells, of which slightly more than 95% were within 22 km of the continental shore. We also filtered for presence of ADPE and EMPE at a large spatial scale. This filter was necessary because there are long stretches of Antarctic coastline where there are no clusters

of ADPE colonies, and no EMPE colonies, which are evenly distributed along the coast (44). Testing for an effect of penguin colony size or distance on seal presence must be conditional on a seal haul-out being present within the foraging range of a colony. In total, 222 locations having WESEs were filtered out for lack of covariate data or for being very small and >22 km away from the continent (i.e., outliers of the distribution of locations versus distance to shore). These represented <5% of the total population of seals that we

counted. Upon filtering locations without seals within 22 km from the continental shore, we arrived at 19,896 grid cells of which only 1462 (or 7%) had seals.

We sought to understand what habitat conditions are strongly associated with the presence of seals in a cell, and if those cells without detected seals are areas with poor-quality WESE habitat. However, fitting a model with 95% of the cells being 0's would result in a fit in which error in correct assignation of sites with seal presence is trivial compared to the error in estimation of sites without seals. To force the logistic model to estimate covariate effects on seal presence and seal absence, we used a balanced dataset by taking 100 bootstrap samples of locations without seals of equal size to the number of locations with seals. Thus, we computed a logistic model 100 times, once with each of 100 bootstrap samples. We averaged regression coefficient values and z values to measure the size of effects and the proportion of values with $P < 0.05$ in the set of 100 samples to assess statistical significance.

We evaluated goodness-of-fit of the combined bootstrap results and explored the utility of adding quadratic terms for improving the fit for all relevant covariates. We then controlled for our a priori-identified four regions [Amundsen Sea, Weddell Sea, East Antarctica, and Ross Sea, with the latter being our reference region so that we could directly compare to previous work in (28)]. Given that we had several candidate models and wanted to control for regional, ice, and penguin effects, we compared the goodness-of-fit for all candidate model outputs by likelihood ratio tests. After selecting the best candidate model, we created partial dependence plots to quantify and visualize covariate effects. All data, R analysis code, and further details can be found at <https://doi.org/10.5281/zenodo.5338593>.

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