Geographic Structuring of Antarctic Penguin Populations

Jarrod A. Santora[1, 2, 3*], Michelle A. LaRue[3, 4] and David G. Ainley[2]

[1]Department of Applied Mathematics, University of California, Santa Cruz, California, 95060, USA

[2]H. T. Harvey and Associates Ecological Consultants, Los Gatos, California 95032, USA

[3]Fisheries Ecology Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 110 McAllister Way, Santa Cruz, CA, 95060, USA

[4]Department of Earth Sciences, University of Minnesota, Minneapolis, MN 55455, USA5

[5]Gateway Antarctica, Department of Geography, University of Canterbury, Christchurch NZ6

*Corresponding E-mail: jsantora@ucsc.edu

Acknowledgements: This study was funded by a grant from the U.S. National Science Foundation, PRL 1543541, and a grant from the Hogwart's Running Club administered through the Antarctic and Southern Ocean Coalition, with Claire Christian managing that arrangement. We thank S. Stammerjohn and A. Leventer for their advice on polynyas and their prevalence in current and geologic time. We also thank 3 anonymous reviewers for their constructive and insightful feedback.

Biosketch: Jarrod A. Santora is an Associate Researcher at the University of California Santa Cruz and studies comparative ecosystem oceanography using statistical and numerical modeling techniques to promote effective conservation and management of marine ecosystems.

DR. JARROD SANTORA (Orcid ID : 0000-0002-5991-4283)

Article type : Research Papers

Abstract:

Aim: We hypothesized that regional spatial organization of Antarctic penguin breeding populations was affected by social factors, i.e., proximity and size of adjacent colonies, and by physical factors, i.e., availability of breeding habitat and proximity of polynyas and submarine canyons where prey is abundant. The hypothesis of Furness & Birkhead (1984), that forage competition and density-dependence affect geographic structure of seabird populations, was tested previously for Antarctic penguins when biologging to quantify colony foraging areas was less common and when assessments of colony size reflected a compendium of historical counts. These data on foraging areas and colony size are now available following 20 years of frequent biologging and real-time satellite data on colony locations and sizes.

Location: Antarctica

Major taxa studied: Penguin species

Time period: Present day

Methods: We prepared a literature summary on the basis of biologging studies to improve assessment of foraging ranges. We collated colony sizes from recent sources and integrated them with data on submarine canyon systems and polynyas. We used geospatial models to assess the relations of the latter features to colony size, clustering, and distribution around Antarctica.

Results: The equal spacing of emperor penguin colonies was constant, with spacing a function of foraging range. In contrast, colonies of other penguin species were clustered, with small colonies adjacent to one another and within outer edge of the foraging area of large colonies. Colonies and especially clusters occurred near polynyas and canyons around Antarctica.

Main conclusions: Density-dependent processes and geography explained penguin colony distribution. We conclude that inter- and intraspecific trophic competition affects a geographic structuring of colony distribution and size, although not necessarily in the same way among species. Results are relevant to assessing effects of climate, ecosystem dynamics, fisheries, and other factors on penguin population trends at regional scales. We suggest that considering penguin colony distribution and abundance at the regional or cluster level is necessary to understand changes in these attributes.

Key words: biogeography, penguin colony, polynya, submarine canyon, trophic competition

INTRODUCTION

Characterizing the size and distribution of populations in coastal ocean ecosystems is challenging because upper trophic level species (i.e. seabirds and mammals) are spatially aggregated as a result of their colonial breeding, central-place foraging behavior, and concentration of their prey (Orians & Pearson, 1979). Competition for prey in waters adjacent to breeding colonies can be intense, leading to a positive relation between the size and foraging area of a colony (Jovani et al., 2015). Trophic competition among neighboring colonies may also structure coastal foraging areas. For instance, where prey availability varies spatially within a region, so does the distribution and size of colonies (Fraser & Trivelpiece, 1996; Sandvik et al. 2016; Ainley et al., 2018). However, where nesting space is not a limiting factor and food availability is homogeneous, prey depletion, which can be significant at large and density-dependent colonies (Lewis et al., 2001; Ainley et al., 2003, 2015), can affect the size and distribution of seabird colonies within the foraging range of large, conspecific and mixed-species seabird colonies (Furness & Birkhead, 1984; Cairns, 1989; Wakefield et al., 2017; Bolton et al., 2019).

Consistent with Furness & Birkhead (1984), there is a positive correlation between population size (i.e., number of breeding pairs) of a seabird colony and the size of its foraging area (Jovani et al., 2015), but a negative correlation with between the population size of the reference colony and that of all other seabird colonies within its foraging range (i.e., a colony's "foraging halo"; Ashmole, 1963). Foraging area size changes as food availability (Pichegru et al., 2010), size of foraging habitat (Cairns, 1989), energetic needs of chicks (Ainley et al., 2004, 2018; Wakefield et al., 2011; Ford et al., 2015), or species-specific flight ability (Pennycuick et al., 1984). Furness & Birkhead (1984) found evidence for their prediction among four seabird species nesting in Britain, although they could not distinguish effects of exploitative and interference competition on prey availability. In addition, Furness & Birkhead (1984) hypothesized that prey would not be depleted in regions where prey are seasonally quite abundant, as in polar regions compared to temperate and especially tropical regions. Evidence consistent with the Furness-Birkhead prediction was reported for many species, mainly in non-polar regions (Bolton et al. 2019). Bolton et al. (2019) found that the degree to which among-colony competition resulted from adjacent (Cairns 1989) or overlapping foraging areas (Furness & Birkhead, 1984) depend in part on species and the size of the reference colony.

The Furness-Birkhead geographic structuring theory was tested in the Antarctic during the crèche period of three pygoscelid penguin species (Ainley et al., 1995). During the crèche period both parents forage simultaneously to sustain rapidly growing chicks and increased feeding frequency is critical to adequate chick growth (Chapman et al., 2011). Also during the crèche period, penguins place the greatest pressure on prey, which are concentrated in both space and time (Ford et al., 2015). During the incubation period, maximum foraging distance from the colony can be greater (Wienecke & Robertson, 1997; Ford et al., 2015; Raymond et al., 2015), but there is less intraspecific pressure among single members of pairs that are foraging. Instead, the main pressure is to forage adequately to maintain or renew individual body condition; fasting mates with their own fat reserves are prepared for irregular return of partners (Ainley, 2002).

A test of geographic structuring of Adélie (*Pygoscelis adeliae*) and gentoo penguins (*P. papua*) in two sectors of the Antarctic, relatively robust data on colony size were available (Woehler 1993), did not detect a negative correlation between neighboring colony size and size of the reference colony's foraging range (Ainley et al., 1995). These findings did not support the geographich structuring theory but the hypothesis that such structure does not occur where prey are quite abundant. A significant negative correlation was detected for Adélies at 150 and 200 km, well beyond what was known then to be the maximum foraging range (Trivelpiece et al., 1987). That is, there was a neighboring colonies farther from the large, reference colony were small. Contrary to theory, there was a significant positive correlation between colony size and the number of breeding individuals of chinstrap penguins (*P. antarcticus*) within their then-known foraging range (50 km). As with the other pygoscelid species, the correlations became more negative at greater distances.

In the early 1990s, information on penguin colony size in any region was a compilation of counts conducted by different methods in different years (sometimes decades apart). In addition, the era of bio-logging of seabird foraging was new. Information on foraging range was sparse, generated by just one study of a group of colonies where three species breed sympatrically (Trivelpiece et al., 1987). Many penguin bio-logging studies have since found that foraging ranges can be much greater than reported by Trivelpiece et al. (1987) (Table S.1). Moreover, with advances in satellite imagery, recent determinations of colony size have been ground-validated (Fretwell et al., 2012; Schwaller et al., 2013; LaRue et al. 2014a; Lynch & LaRue 2014). Therefore, we revisited whether there is geographic structuring among Antarctic penguins, including the emperor penguin (*Aptenodytes forsteri*) and the three pygoscelid species.

We also evaluated relations between penguin colony location and sizes across the continent and oceanographic factors, such as proximity to polynyas (Massom et al., 1998; Ainley, 2002; Arrigo & van Dijken, 2003) and upwelling centers (e.g., shelfbreak, submarine canyons; Fraser & Trivelpience, 1996; Oliver et al., 2013; Schofield et al., 2013; Santora et al., 2018). High-latitude polynyas are persistent openings in sea ice that are driven by winds and ocean currents. The interaction among ocean currents, submarine canyons, and polynyas promotes elevated and persistent regional biological productivity and influences aggregation intensity of prey and predators. Therefore, they may influence seabird colony distribution patterns (Ainley et al., 2003; Sandvik et al., 2016; Bolton et al., 2019). For example, upwelling of nutrient-rich circumpolar deep water (CDW) within canyons positively affects food availability, and currents within canyons concentrate prey (Ainley et al., 2004; Oliver et al., 2013; Santora et al., 2018). Furthermore, open water or loose pack ice within high-latitude polynyas facilitates penguin foraging in areas where sea ice is regionally prevalent (Ainley, 2002).

At the extent of Antarctica, we tested the hypothesis that large penguin colonies affect the size and distribution of other colonies within foraging areas that overlap. In other words, we tested whether only small colonies exist within the foraging range of a large colony. We evaluate whether foraging area increases as colony size increases; whether the size and distance of neighboring colonies, and the distance from a polynya or submarine canyon, is associated with the size of a focal colony and whether spacing of penguin colonies can be explained by social factors, such as intraspecific competition for food, rather than physical factors. We conducted an analysis of penguin tracking studies to assess species foraging range and to inform our geographic assessment of colony distribution. We assessed colony distribution and clustering (even spacing versus aggregation) with geospatial models and spatial statistics. Due to differences in natural history and distribution, we conducted different analyses for high latitude, sea ice obligate species (Adélie and emperor penguins) and lower latitude coastal species (gentoo and chinstrap penguins, but only on the Antarctic Peninsula, fo which data are the most complete). Our analysis may inform interpretation of trends in recently assessed regional populations of these species (Barber-Meyer et al., 2008; Lynch et al., 2012; Southwell et al., 2015). Although clusters of colonies may function as meta-populations (Dugger et al., 2010; LaRue et al., 2013, 2014b), growth rates may vary among clustered colonies (Lyver et al., 2014; Dugger et al., 2014). Therefore, a single colony could be misleading.

METHODS

Data selection. We considered only the high latitude Antarctic. Data on the location and size of emperor and Adélie colonies were collected around the continent, whereas data on chinstrap and Gentoo colonies were collected from the Antarctic Peninsula region and southern Scotia Sea, the high latitude portion of those species' ranges. Information on location and size of emperor colonies was derived from visual inspection of high-resolution satellite images taken since 2009 (Fretwell et al., 2012; LaRue et al., 2015). Data on Adélie penguins, from 2008-2013 were gathered by Lynch & LaRue (2014) through similar analysis of high-resolution imagery. We compared the latter compilation with that of Schwaller et al. (2013), who used Landsat imagery of guano footprints (1999-2003) to estimate Adélie abundances. Therefore, we inserted breeding sites not in Lynch & LaRue (2014) but in Schwaller et al. (2013) into the Lynch & LaRue (2014) data. Both Lynch & LaRue (2014) and Schwaller et al. (2013) used estimates of nest density and then GIS and the number of satellite pixels to estimate the number of nests at a given location as a function of occupied breeding area (LaRue et al., 2014). Populations of Adélie and emperor penguins are good candidates for assessment via high-resolution satellite imagery due to their body size (e.g., emperor penguins), location of colonies on an open landscape, and contrast with surrounding areas (LaRue et al., 2016). We acknowledge the possibility that we did not identify a few small colonies. We used data on gentoo and chinstrap penguins from MAPPPD (Mapping Application for Penguin Populations and Projected Dynamics; Humphries et al., 2017). See the Supplemental Methods for additional information on penguin species breeding habitat.

Definition of colony. Given the apparent clustering and geographic structure (regional versus continental) of different Antarctic penguin species, we applied colony definitions relevant to each. Definition was easiest for emperor penguins because their colonies are relatively few. Therefore any location where they occur during the breeding season coincides with a colony. Fast ice, which is needed for formation of their colonies, is not limited around Antarctica. For the Pygoscelids, all of which have clusters of land-based breeding sites, we adopted the definition of a breeding colony in Ainley (2002) and Lynch and LaRue (2014): breeding sites [as defined by Lynch et al. (2012)] within a 5 km radius. We selected the 5 km radius on the basis of three criteria: the areal extent of the largest Adélie penguin breeding sites (e.g., Cape Crozier at 2 km X 3 km); banding recovery data in the Ross and Beaufort Island meta-population (Dugger et al., 2010; LaRue et al., 2013); and evidence of rapid, extensive regional gene flow (Shepherd et al., 2005; Gorman et al., 2017). Breeding sites could stretch along a coast, such as at Cape Bird, Ross Island, where 1-2 km separate each of three assemblages of subcolonies (all of which use the same landing beach), or could be on different islets or islands within that radius, such as those in Arthur Harbor, Anvers Island. Although no genetic studies have investigated the relatedness of nearby breeding sites, banding indicates extensive expansion of individuals from original banding locations at the extent of what define as a colony (See the Supplemental Methods S.1 for a description of banding and re-sighting).

Previous studies indicated that gentoo and chinstrap penguin colonies are highly aggregated (Ainley et al., 1995; Lynch et al., 2012). There are no emigration or immigration data for either species, so we again defined as a colony as all breeding sites within a 5 km radius with overlapping foraging radii. We used the polygon dissolve method in ArcView to merge colony aggregates within overlapping 5 km radius buffers. We excluded sites of <110 breeding pairs of Pygoscelids because the probability of extirpation increases as isolation increases and as abundance decreases (Lynch & LaRue, 2014). Therfore, we assumed that these few locations would have little effect on our analysis. We calculated the centroid and nearest distance from the centroid to neighboring colony aggregates.

Marine geology and polynya data. We used global data on marine geology that encompasses the margins of the continental slope and shelf, distribution of glacial troughs, and the distribution and dimensions of submarine canyon systems (Harris et al., 2014; Figure 1). The resolution of bathymetry for the Antarctic continental shelf and slope is 50 and 100 m, respectively, and satellite gravity data had a resolution of 12.5 km. We derived the location, dimensions, and aspects of high-latitude, latent-heat polynyas from Arrigo et al. (2015). We used a GIS to measure the distance (km) from Adélie and emperor penguin colonies to the edge of a polynya and head of submarine canyon (Supplemental Methods).

Analytical approach. For each penguin colony, we measured the nearest distance (km) to each conspecific neighboring colony (emperor and Adélie) or colony aggregate (gentoo and chinstrap), and noted colony size. We used the 2-dimensional Global Moran's *I* spatial autocorrelation test (Bivand et al., 2008) to test whether penguin colonies were clustered or evenly spaced on the basis of geographic distribution and colony size. The Moran's *I* test computes the mean and variance for all colonies and generates their mean deviation, and for all neighboring colonies based on a distance band specified by their distribution. The resulting test, a normalized index (by variance), provides a measure of whether colonies of a given size class are clustered (positive value), large colonies tend to be located near smaller colonies (negative value), or colonies are evenly spaced (non-significant). For the high latitude and ice-obligate species that breed continent-wide, we drew buffers, which we refer to as neighborhoods, around each colony that corresponded to foraging radii: 50, 100, 150 and 200 km (Ainley et al., 1995; Table S.1). We evaluated the relative clustering of Adélie and emperor penguin colonies at each of these radii by determining the percent of neighborhoods that overlapped.

We evaluated whether colony size and distance of neighboring colonies, and the distance from a polynya or submarine canyon, were associated with the size of a focal colony for emperor and Adélie penguins. We used generalized additive models (GAMs) to evaluate the relations with nearest colony size and distance, and with distance to polynyas and submarine canyons. We selected GAMs given their flexibility to identify non-linear functional relations between species distribution and environmental conditions (Zuur et al., 2009). The GAM implemented for Adélie and emperor penguins was: colony size = *s*(nearest colony size) + *s*(distance to nearest colony) + *s*(distance to polynya) + *s*(distance to canyon) + *te*(Lon, lat); where *s* is a smooth regression spline and *te* is a tensor product that accounts for spatial autocorrelation. Due to the clustering and appreciable variation of colony sizes, we specified GAMs for Adélie and emperor penguin colony size as a Poisson distribution and a log-link function. We implemented GAMs with the *mgcv* package in R (R Development Core Team, 2018), and estimated smoothness parameters with generalized cross-validation; we used adjusted R^2 and percent deviance explained to evaluate model performance (Zuur et al., 2009).

To describe the geographic structuring of gentoo and chinstrap penguin colonies, we examined their colony aggregates (clusters; as noted above) and calculated their mean, maximum, and total population size, and the distance to the nearest colony cluster (or individual colony) and its attributes. We did not relate these species' colony aggregates to the presence of polynyas or submarine canyons due to their strong regional association in the Antarctic Peninsula and South Orkneys. Nearly all penguin colonies in the western Antarctic Peninsula are within the vicinity of steep bathymetry and submarine canyons and troughs

(Fraser & Trivelpiece 1996; Schofield et al., 2013; Figure 1), and with little sea ice during spring and summer, there are no polynyas (Arrigo et al. 2003, 2015). If there was sea ice, then sensible heat polynyas would be associated with canyons (Scofield et al., 2017). Because all three pygoscelid penguin species occur within the Antarctic Peninsula region, we examined the spatial overlap and segregation of their colonies. We spatially resolved pairs of colonies, or aggregates (clusters) of colonies for gentoo, chinstrap and Adélie penguins, with the same polygon dissolution method generated an overlap index (% co-occurrence) to visualize spatial patterns. The spatial overlap provides a simple index of the percentage of colonies that overlap among species. Our assessment does not address whether the presence of a give species' colony is associated with the presence of another species.

RESULTS

*Colony size and foraging area size***.** Data on penguin colony sizes and biologging has changed understanding of penguin foraging area (Table S.1). For Adélie penguin, colony foraging range during the chick crèche period expanded as a function of colony size: $y=0.280x^{0.54}$, $R^2=0.85$, $p<0.001$ (Figure 2). Therefore, for a colony of 5000 breeding pairs, maximum foraging range appeared to be ~30 km, but for a colony of 150,000 pairs, it reached >180 km to the sea. Foraging range data for gentoo and chinstrap penguins are far less abundant, and there are no data from the largest colonies. Although there are chinstrap colonies as large as 225,000 pairs, biologging has been conducted only at colonies from 250-13,000 pairs; gentoo colonies reach 10,000 pairs, but biologging has been conducted only at those with 300-4,500 pairs (Miller et al., 2010; Cimino et al., 2016a). The relation between foraging range and colony size was linear in relatively small colonies; for chinstrap, $y=0.0023x+23.9$ ($R^2=0.66$), and for gentoo, $y=0.0017x+22.5$ ($R^2=0.34$), both $p<0.05$. A colony of 5000 chinstrap pairs forages within ~30 km, and a colony of 13,000 pairs forages to 60 km. The largest studied colony of gentoo penguins (4500 pairs), had a 30 km foraging range, but colonies of <1000 pairs had a 20-24 km range (Table S.1). We expect that the largest chinstrap and gentoo colonies would forage much further away. Biologging of emperor penguins has been infrequent and the sample size of instrumented birds has been low (for the four studies during crèche: n=1, 2, 5 and 15).

Nevertheless, it appears that during crèche emperor parents may forage out hundreds of kilometers (Table S.1).

Emperor penguin. This species occurred in 54 colonies spaced an average of 220±17 km apart. Colonies were relatively evenly spaced (I=0.14, z=1.29, p=0.19). Most colonies colony was geographically associated with a coastal polynya and cross-shelf canyon (R^2=0.60; deviance explained=49.9%; Figure 3). The majority of emperor penguin colonies were within 100 km of a polynya and 200 km of a submarine canyon system, which is within their foraging range (Table S.1). Because few colonies were further than 100 km and 200 km from a polynya or canyons, respectively, the strength of the relation decreased at greater distances It is unknown whether these latter colonies were associated with sensible heat processes, e.g., persistent flaw leads. Trophic competition appeared to play a greater role as the neighborhood around the colonies increased. The colonies were not clumped and the radii of approximately 35% of colonies overlapped within the 100-150 km range, consistent with foraging range (Table S.1, Figure S.2).

Adélie penguin. This species occurred in 189 colonies and colonies were significantly clustered (I=0.06, z=3.35, p<0.01). Colonies were highly clumped, with average spacing of 35±6.2 km, but with large gaps between clumps (Figure 4). Clumps included smaller colonies in proximity to at least one large colony (Figure S.3). In general, colonies occurred in close proximity within <200 km; 102 colonies had overlapping 50 km halos. GAMs indicated that the effect of nearest colony size was strongest at >50,000 pairs (i.e., hump-shaped), and the effect of large colonies was greatest within a 200 km neighborhood of colony clusters (Figures 5a-b, S.3). Therefore, the majority of colonies were within 200 km, with a strong effect at 50-100 km. Two colonies are relatively isolated (Figure 5b). Adélie colonies were associated with submarine canyons and polynyas (R^2=0.60; deviance explained=68.4%; Figure 5c-d). There was a strong association between colony size and canyons within 100 km of colonies. Fifty percent of the colonies were within 100 km of a canyon, whereas the remaining 15 colonies were 300-500 km away from a canyon. Most colonies were within 50 km of a polynya, most of which are small and associated with a narrow continental shelf (with exception of the Ross Sea; Figures 1, 5d).

Chinstrap penguin. Colonies of this species were highly aggregated, and most were concentrated on islands in the Antarctic Peninsula region (Figure 6). Chinstrap penguin colonies were significantly clustered (*I*=0.11, z=4.62, p<0.01). Chinstrap penguins occurred in 254 colonies, corresponding to 35 distinct colony clusters (Figure S.4). These clusters were highly aggregated within the Antarctic Peninsula region (33 clusters) and the South Orkneys (2 of the largest clusters). Among the 35 chinstrap penguin colony clusters, 54% contained 2-4 colonies, 34% contained 5-10 colonies, and 11% contained 16-51 colonies. The 4 largest colony clusters represent a major percentage (55%) of the total population and therefore may be considered meta-colony locations. Due to the intense aggregation of major colony clusters and their spatial distribution, the size and spacing of chinstrap penguin colony clusters is varied (Figure S.4). The mean and standard deviation of separation distance across colony clusters was 33.10±18.71 km and the mean separation distance of the largest four was 54.79±26.37 km.

Gentoo penguin. This species occurred in 85 colonies, 69 of which were in 16 clusters (Figures 6, S.5). Gentoo penguin colonies were significantly clustered (*I*=0.09, z=3.52, p<0.01),and less aggregated than those of chinstrap penguins (Figures 6, S.4-S.5). Fifty percent of clusters contained 2 colonies, 31% contained 3-5 colonies, and 19% contained 9-14 colonies. The 4 largest colony clusters represent 26% of the total population (Figures 6, S.5). The mean and standard deviation of separation distance for all colony clusters was 22.06±13.01 km, and that of the largest 3 colony clusters was 23.20±15.89 km. Regardless of the number of colonies, gentoo clusters are closer than chinstrap penguin colony clusters.

Spatial overlap of pygoscelid species. Colonies of three pygoscelid species occur almost entirely in the Antarctic Peninsula region and have varying degrees of spatial overlap and segregation. Chinstrap penguin colonies are highly aggregated throughout the South Shetland archipelago, with more colonies on the north side of the islands (Figure 6). Smaller chinstrap penguin colonies are located along the western Antarctic Peninsula, especially within Gerlache Strait (Figure 6). Gentoo colonies are also in the South Shetlands but are mostly concentrated along the inner Bransfield Strait (Figure 6). Chinstrap and gentoo colony clusters overlap at 22 locations, and are generally spatially segregated. For instance, there are no chinstrap colony clusters located in the northern Antarctic Peninsula region, where gentoo colonies are concentrated, and only 4 small chinstrap colonies co-occur in the highly concentrated gentoo colony clusters in southern Gerlache and around Anvers Island (Figure 6). Chinstrap penguin colonies are more segregated from Adélie penguin colonies, with only 11 colony clusters overlapping: 7 in the South Shetlands, two along the Antarctic Peninsula, and one on Anvers Island (Figure 6). Gentoo and Adélie penguin colonies overlapped in 21 locations, most notably on the northern Antarctic Peninsula and southern side of King George Island (Figure 6).

DISCUSSION

Relations between colony distribution and intraspecific trophic competition and habitat availability

Over the past 25 years, substantial advances in satellite technology and methods, and increased effort to describe the distribution of extant seabird colonies and species and colony-specific foraging range (noted by Bolton et al., 2019), permitted a new macro-ecological examination of how Antarctic penguin colonies are geographically structured. Contrary to Ainley et al. (1995) our results show strong geographical structuring among Antarctic penguins, consistent with the main Furness & Birkhead (1984) and Cairns (1989) hypothesis. Even in the Antarctic, where food is abundant, geographic structuring is evident. In the mid-1990s, data on penguin colony size and foraging range were insufficient to address this issue. Satellite remote sensing and biologging have improved the available data greatly, except perhaps for emperor penguins. At the low end of the colony size range, all foraging distance of all 3 pygoscelids increases linearly as colony size increases. We believe that geographic structuring is driven by intraspecific trophic competition. In a well-studied cluster of 4 Adélie penguin colonies at Ross and Beaufort islands, Ross Sea (Ainley et al., 2004; Dugger et al., 2010; LaRue et al., 2013), the foraging area of the large colony abutted those of the smaller colonies, and displaced them as chicks grew and foraging intensified. The foraging areas of the small colonies in the Ross and

Beaufort cluster, however, overlapped (Ainley et al., 2004; Ford et al., 2015). This is the only location where foraging among all islands of a colony cluster has occurred. There appears to be a foraging density at which a large colony displaces the foraging areas of neighboring colonies. We expect geostructuring to affect contemporary changes in the sizes of populations (Lynch et al., 2012; Cimino et al., 2013, 2016a,b; Lyver et al., 2014; Southwell et al., 2015) that are driven by regional ecosystem changes rather than local human disturbance.

The clustering of Adélie penguin colonies is not entirely based on physiographic features. We found only small colonies within a ~200 km foraging range of large colonies, such as the Cape Crozier colony, one of the three largest (Lynch & LaRue, 2014). The distribution of Adélie penguin colonies is associated with breeding habitat, which is rare in the Antarctic; 0.18% is ice free (Chown et al., 2017). However, along the west Antarctic Peninsula and coast of Victoria Land, where most of the ice-free terrain is located, Adélie colonies occur in clusters, with some ice-free, potential nesting habitat vacant (Emslie et al., 2003, 2007). A possible explanation is that Adélie penguin colonies are also associated with cross-shelf canyons and troughs and coastal polynyas, and the vacant habitat is too distant from marginal ice zones of polynyas (Emslie et al., 2003). Although the association, in part, is related to the nutrient-rich CDW upwelled along the shelf-break and then advected up canyons onto the continental shelf (Dinniman et al., 2011), thus supporting the food web (Schofield et al., 2013; Santora et al., 2017), levels of primary production in latent-heat polynyas are likely not a factor. The latter is consistent with Dugger et al. (2014) and contrary to the hypothesis of Arrigo et al. (2015). Most production in latent-heat polynyas results from algal species that do not contribute to penguins' food web (Smith et al., 2014). By contrast, in the few sensible-heat polynyas, or in the upwelling related to troughs of the western Antarctic Peninsula, there is no wind-driven turbulence and diatoms are abundant (Kavanaugh et al., 2015; Schofield et al., 2017). We speculate that polynya size affects the amount of marginal ice zone habitat and the abundance of diatoms (Smith et al., 2014). Polynya persistence is important, especially in spring, because Adélie penguins need open water (Trivelpiece et al., 1987; Ainley, 2002; Dugger et al., 2014; Emslie et al., 2003).

Katabatic winds channel down valleys that represent ice streams (Parrish & Bromwich 1987; Figure S.1) and create coastal latent heat polynyas (Arrigo & van Dijken, 2003; Arrigo et al., 2015) that attract Adélie and emperor penguins (Ainley, 2002; Massom et al., 1998). Such polynyas have been present for millennia (Thatje et al., 2008; Mezgec et al., 2017), predating most current Adélie, and possibly emperor, colony locations (Emslie & Woehler, 2005; Emslie et al., 2003, 2007). The ice streams during glacial ice maxima when the Antarctic ice sheets extended across most portions of the Antarctic continental shelf carved the cross-shelf glacial troughs (Anderson, 1999)and lead to the association among coastal valleys, submarine canyons and troughs, and polynyas. Only a few colonies, such as Cape Adare, Ross Sea, or Anvers Island, are associated with sensible-heat polynyas (those maintained by the upwelling of warm CDW) (Jacobs & Comiso, 1989; Thatje et al., 2008). In the western Antarctic Peninsula, intrusion of warmer CDW is a factor in canyon and glacial trough areas (Schofield et al., 2013), where there are several pygoscelid colonies (Figure 6). During winter, with presence of sea-ice and a sensible-heat polynya, the areas also become important to Adélie penguins (Ribic et al., 2008); the other two pygoscelid species, as winter sea-ice shifts north.

The association of emperor penguin colonies with polynyas and cross-shelf submarine canyons and glacial troughs is equally apparent (Massom et al., 1998). We expect that sensible heat processes also play a role, given proximity to troughs and the narrow continental shelf of most of East Antarctica. However, emperor colonies were evenly spaced. Spacing averages ~220 km [Ancel et al. (2017) found 311 km], and the foraging range of this species during crèche apparently is on the order of hundreds of kilometers (Table S.1). Thus, it appears that adjacent colonies avoid overlap. Gaps between colonies certainly contain adequate breeding habitat (areas of protected, persistent fast ice in the vicinity of a polynya) (LaRue et al., 2019). It may be that these gaps are real because few existing colonies were not detected by satellites (Ancel et al., 2017). These gaps may well represent a reserve of habitat to which existing colonies can move should conditions at current colony locations become unfavorable (LaRue et al., 2014; Fretwell and Trathan, 2019), and the move is not too close to an existing, large colony, or possibly too close to a large concentration of Weddell seals, a potential trophic competitor (LaRue et al., 2019).

Application of results

Aggregations of prey beget predator aggregations. Combining information on geographic structure and clustering of penguin colonies and foraging range provides inference on the continental and regional distribution of persistent prey patches. The clustering and spacing of densely clustered penguin colonies along the Antarctic Peninsula indicates a predictable and abundant supply, especially historically (Atkinson et al., 2019). In this region, dense concentrations of Antarctic krill (*Euphausia superba*) are distributed throughout the outer shelf-slope and coastal waters, with high concentrations in frontal zones and associated with canyons and troughs (Santora et al., 2017). Persistent penguin areas are within the vicinity of the largest penguin colony clusters that we identified (chinstrap and gentoo; Santora & Veit, 2013).

We evaluated overlap among colonies of pygoscelid penguin species and found strong spatial segregation and distinct offsets among species, which reflect their life-history and indicating potentially strong interference competition. For example, clusters of chinstrap penguin colonies were considerably offset from gentoo and Adélie penguin colonies (Figure 6), whereas colonies of the latter species overlap more within the northern tip of the Antarctic Peninsula. Gentoo penguin colony clusters, although fewer and smaller than those of other species, occurred in more regions, possibly indicating greater flexibility in nesting and foraging behavior. The majority of penguin colony clusters were concentrated adjacent to submarine canyons and glacial trough systems (Fraser & Trivelpiece, 1996; Ribic et al., 2008; Schofield et al., 2013). Canyons can act as conduits for concentrating krill swarms and mesopelagic fish near penguin colonies (Santora & Reiss 2011). The predictability of krill swarms near penguin colonies also attracts fishing vessels that may deplete krill (Croll & Tershy, 1998). Therefore, the geographic structuring (clustering and spacing) of penguin colonies provides reference points for ecosystem monitoring and fishery management.

Penguin foraging range sometimes is used to inform placement and size of marine protected areas (MPA; Raymond et al., 2015), with the aim of protecting entire foraging areas of colonies. The recently designated Ross Sea Region MPA covers the entire breeding season foraging areas of 12 Adélie and 7 emperor penguin colonies. However, most research on foraging ranges of penguins, except for Adélie penguins, has been confined to small colonies. Therefore, if there are larger, unstudied colonies in a region considered for MPA designation, spatial planning based on penguin foraging range may be inadequate. Moreover, the extent of foraging ranges can change as colony size changes over time (Dugger et al., 2014). Models based on data from small colonies also can overestimate the area in which penguins are foraging (Raymond et al., 2015).

Changes in size of one colony may not be representative of regional trends. For instance, in the metapopulation of four colonies on Beaufort and Ross islands, Ross Sea (Dugger et al., 2010), the longest-monitored colony cluster in the Antarctic, since about 2000, there was a decreasing trend in one colony, followed by a barely increasing trend, whereas the other colonies in the cluster grew at a high rate (Lyver et al., 2014; Dugger et al., 2014). At the Beaufort Island colony, initially there was little growth as most of its pre-recruits emigrated to the growing colonies in the cluster. Around 2010, terrestrial ice fields began to retreat, providing more nesting habitat and discouraging emigration. The size of the Beaufort Island colony began to increase in synchrony with the other two large colonies in the cluster (LaRue et al., 2013). Many Royds colony adults emigrated to Cape Bird upon successive years of breeding failure in the early 2000s, and the Royds colony decreased by half (Dugger et al., 2014). This is similar to what recently happened at the Halley Bay emperor penguin colony, which after successive breeding failure also moved to the next closest colony (Fretwell & Trathan 2019). Therefore, we recommend that any penguin colony size monitoring be conducted within entire colony clusters to avoid misleading extrapolation to regional patterns. Trends at a single colony, could affect its neighbors within its colony cluster.

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Data Accessibility Statement: All data included within this study (penguin colonies and marine geology) are publicly available.

Figures:

Figure 1: (a) Location of coastal latent-heat polynyas (from Arrigo et al., 2015), extent of the continental shelf and slope, glacial troughs and submarine canyons (from Harris et al., 2014) around Antarctica. Map projection is polar stereographic.

Figure 2: Relations between maximum foraging range and colony size in Adélie penguins; the triangle symbol represents results of the first determination of foraging range in this species by Trivelpiece *et al.* (1987), and is the value used by Ainley *et al*. (1995) in the first attempt to investigate geographic structuring in Antarctic penguins. See Table S.1 for summary of literature review.

Figure 3: (a) Distribution of emperor penguin colonies in relation to polynyas and submarine canyons; (b-c) results of GAMs illustrating the functional relationship between (b) colony size and (c) distance to polynya and submarine canyon; thin grey line indicates 95% confidence intervals and black tick marks indicate availability of data on colony size and location. Map projection is polar stereographic.

Figure 4: Distribution and abundance of Adélie penguin colonies in relation to polynyas and submarine canyons. Map projection is polar stereographic.

Figure 5: Results of GAMs for assessing the effect of (a) nearest colony size, (b) distance to nearest colony, (c) distance to submarine canyon and (d) polynya on Adélie penguin colony size and distribution; thin grey line indicates 95% confidence interval and black tick marks indicate availability of data on colony size and location.

Figure 6: Spatial distribution of pygoscelid penguin colony clusters and assessment of their overlap and segregation in the Antarctic Peninsula region: (a) chinstrap and Gentoo, (b) Adélie and chinstrap, and (c) Adélie and gentoo. Map projection is polar stereographic.

Supplemental Materials:

Table S.1 Summary of colony size and known foraging range

Supplemental Methods S.1: Additional detail on (1) consideration of breeding habitat, (2) banding and re-sighting and (3) importance of polynya and submarine canyons

Figure S.1: Coastal latent-heat polynyas and katabatic winds

Figure S.2: Emperor penguin colony neighborhood

Figure S.3: Adélie penguin colony neighborhoods

Figure S.4: Summary of Chinstrap penguin colony clusters

Figure S.5: Summary of Gentoo penguin colony clusters

Figure 1

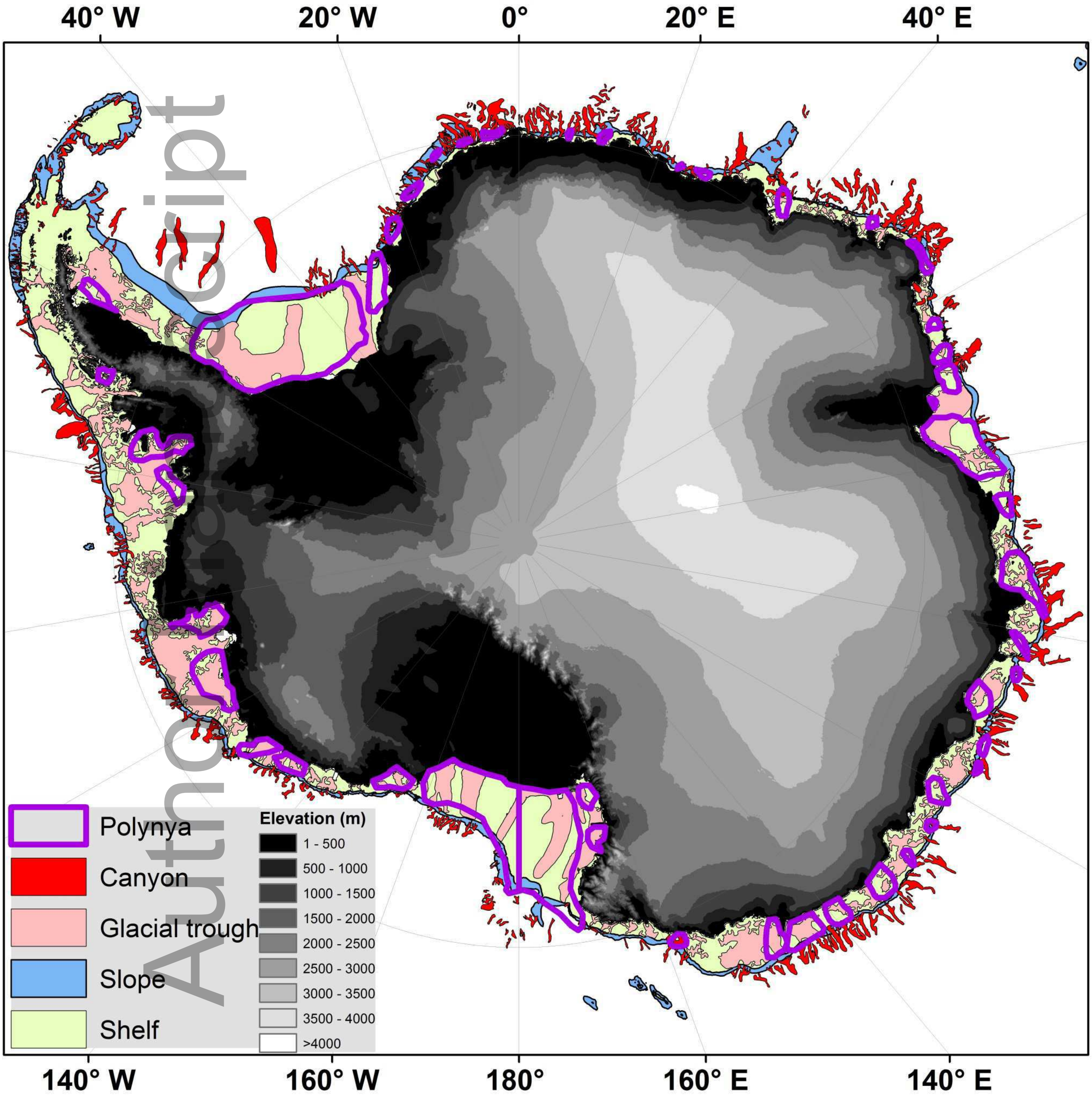

40° W
20° W
0°
20° E
40° E
140° W
160° W
180°
160° E
140° E
Polynya
Canyon
Glacial trough
Slope
Shelf
Elevation (m)
1 - 500
500 - 1000
1000 - 1500
1500 - 2000
2000 - 2500
2500 - 3000
3000 - 3500
3500 - 4000
>4000

Figure 2

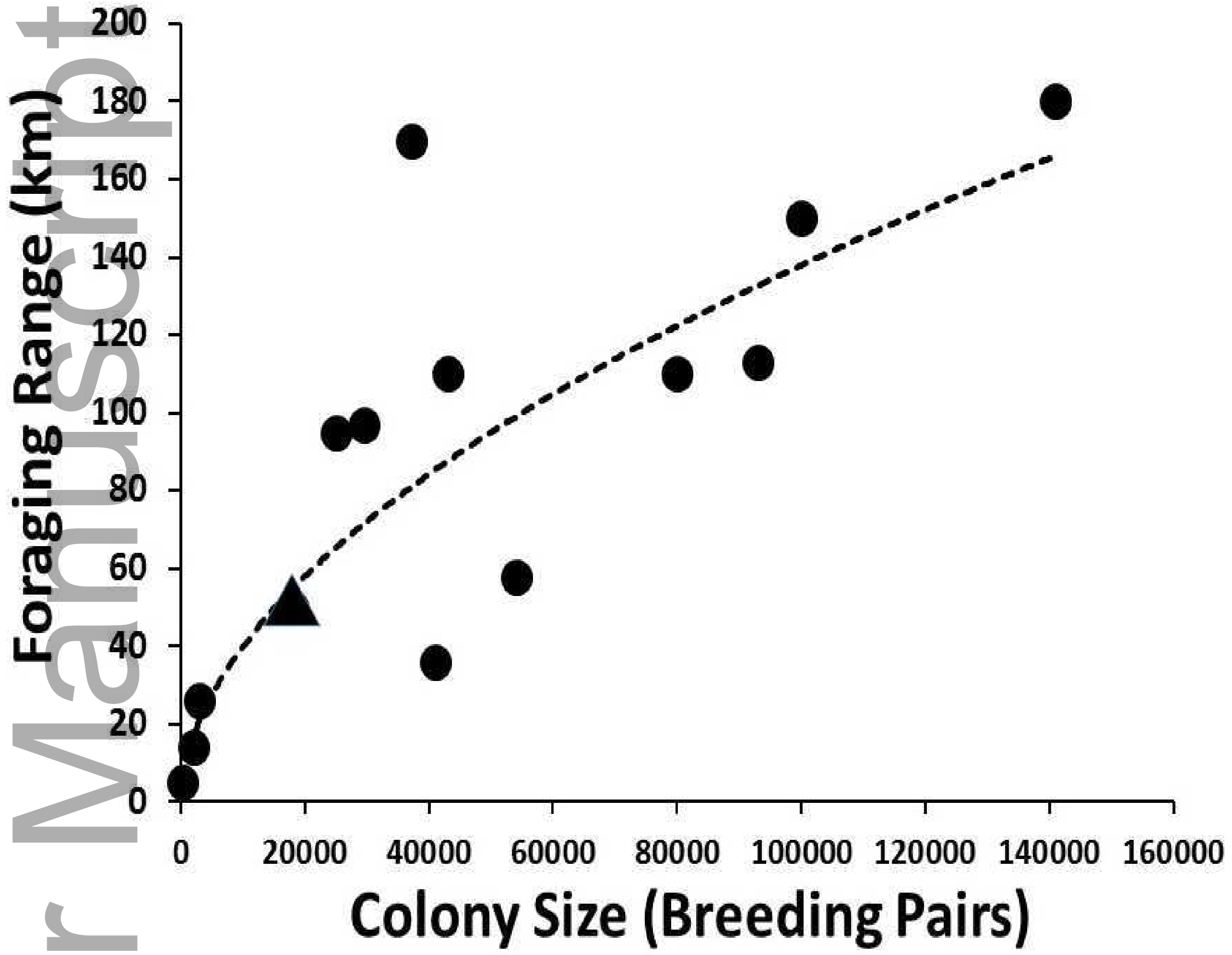

Foraging Range (km)
200
180
160
140
120
100
80
60
40
20
0
0
20000
40000
60000
80000
100000
120000
140000
160000
Colony Size (Breeding Pairs)

Figure 3

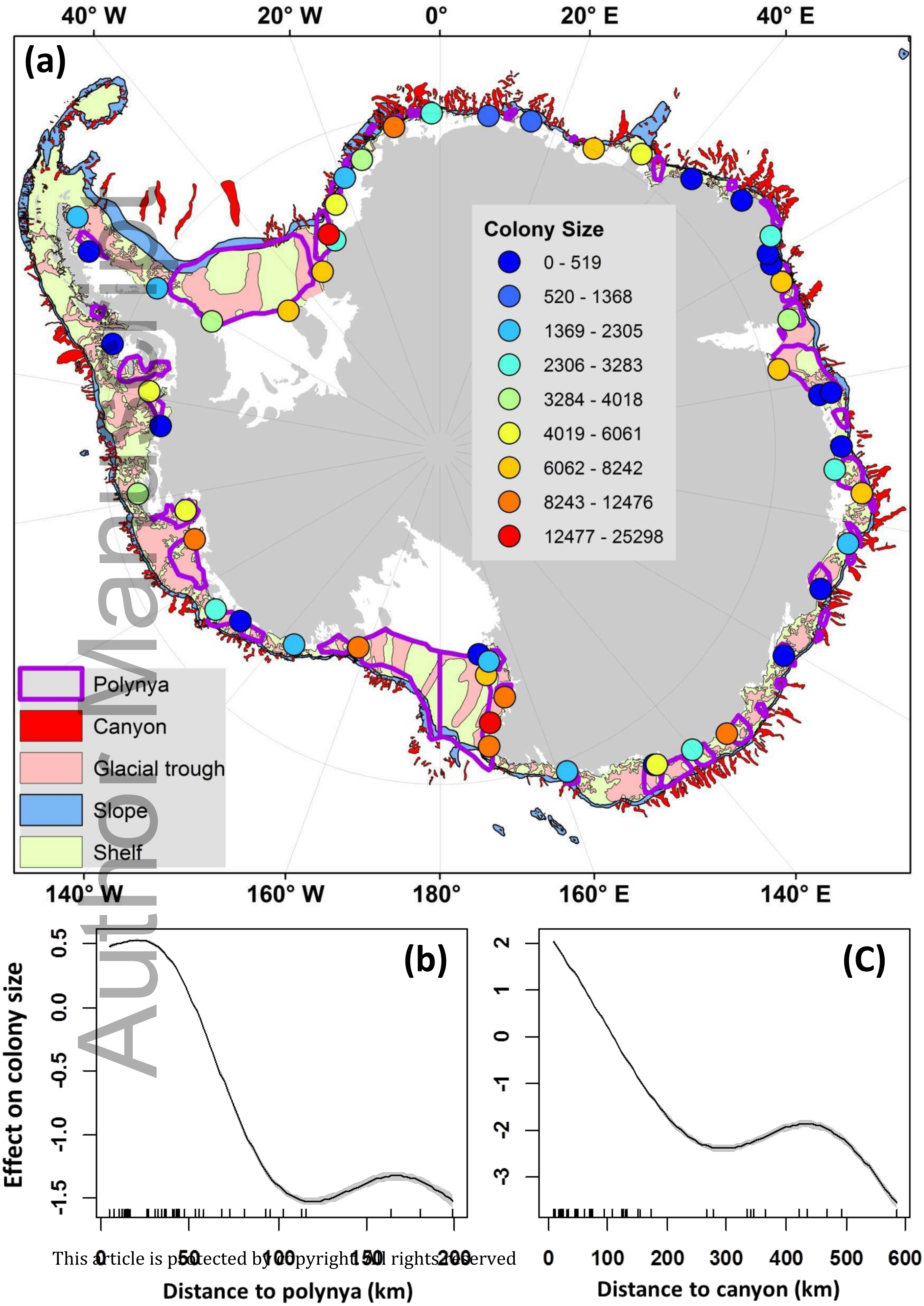

40° W
20° W
0°
20° E
40° E
(a)
Colony Size
0 - 519
520 - 1368
1369 - 2305
2306 - 3283
3284 - 4018
4019 - 6061
6062 - 8242
8243 - 12476
12477 - 25298
Polynya
Canyon
Glacial trough
Slope
Shelf
140° W
160° W
180°
160° E
140° E
(b)
Effect on colony size
0.5
0.0
-0.5
-1.0
-1.5
0
50
100
150
200
Distance to polynya (km)
(C)
2
1
0
-1
-2
-3
0
100
200
300
400
500
600
Distance to canyon (km)

Figure 4

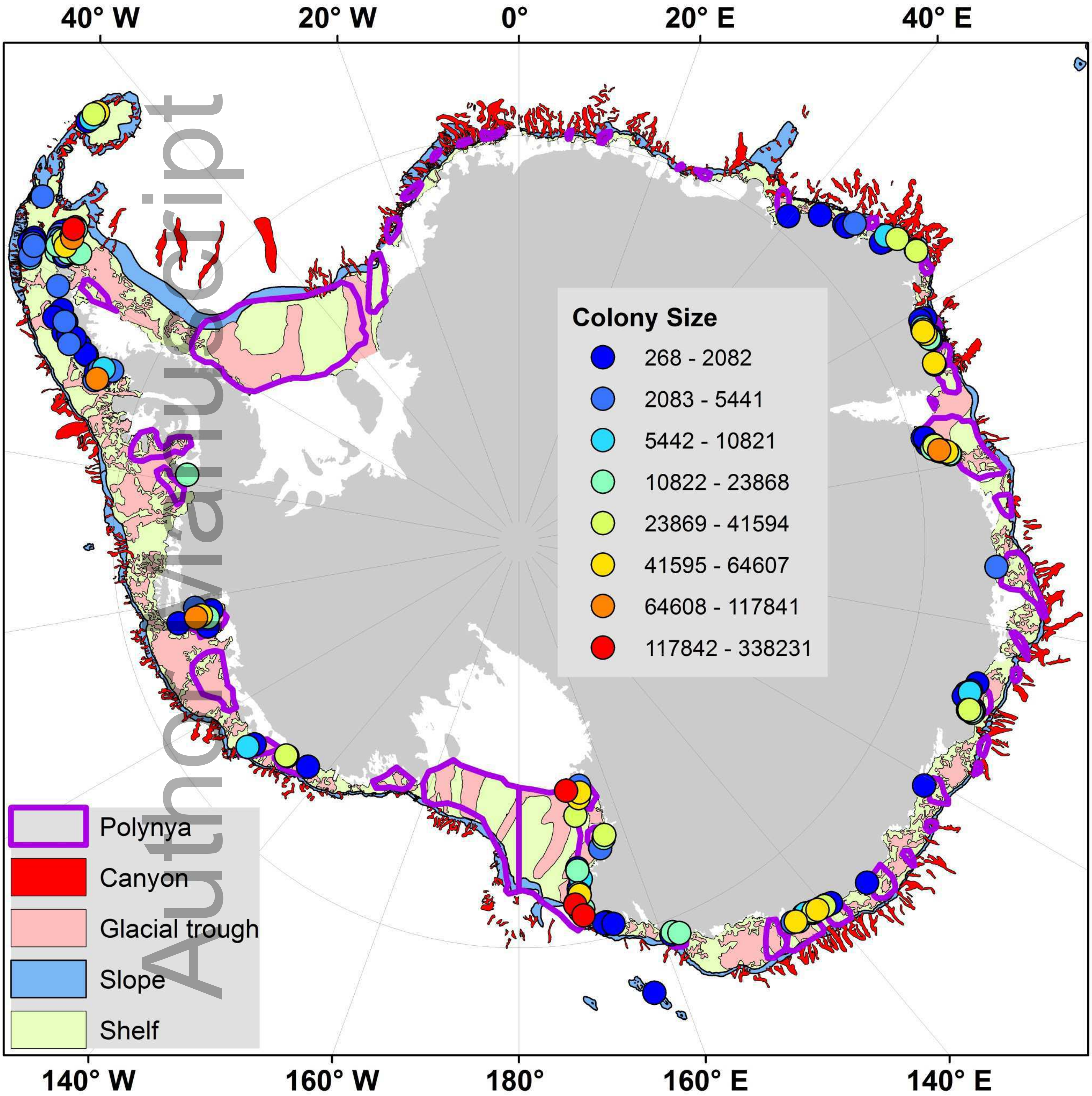

40° W
20° W
0°
20° E
40° E
Colony Size
268 - 2082
2083 - 5441
5442 - 10821
10822 - 23868
23869 - 41594
41595 - 64607
64608 - 117841
117842 - 338231
Polynya
Canyon
Glacial trough
Slope
Shelf
140° W
160° W
180°
160° E
140° E

Figure 5

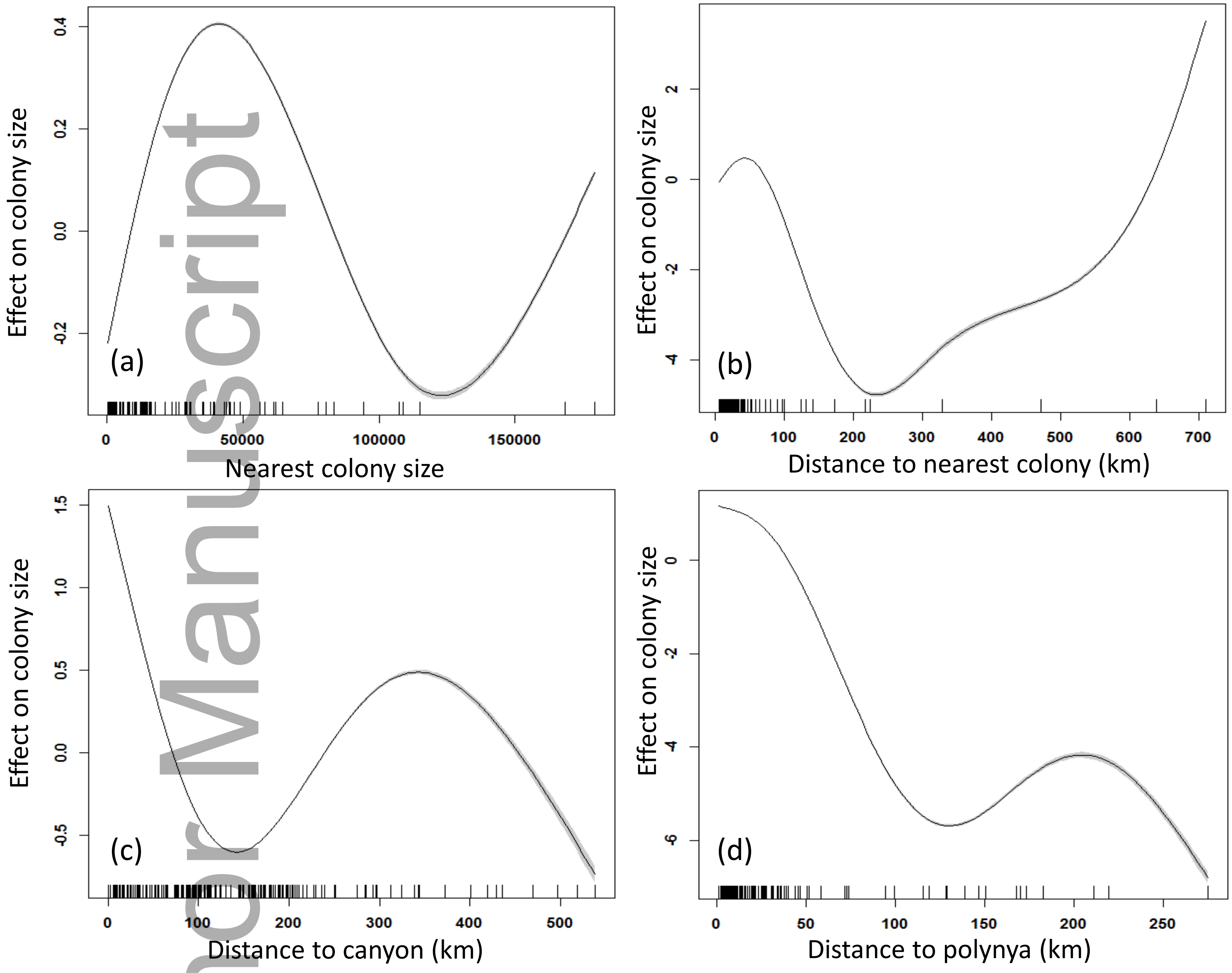
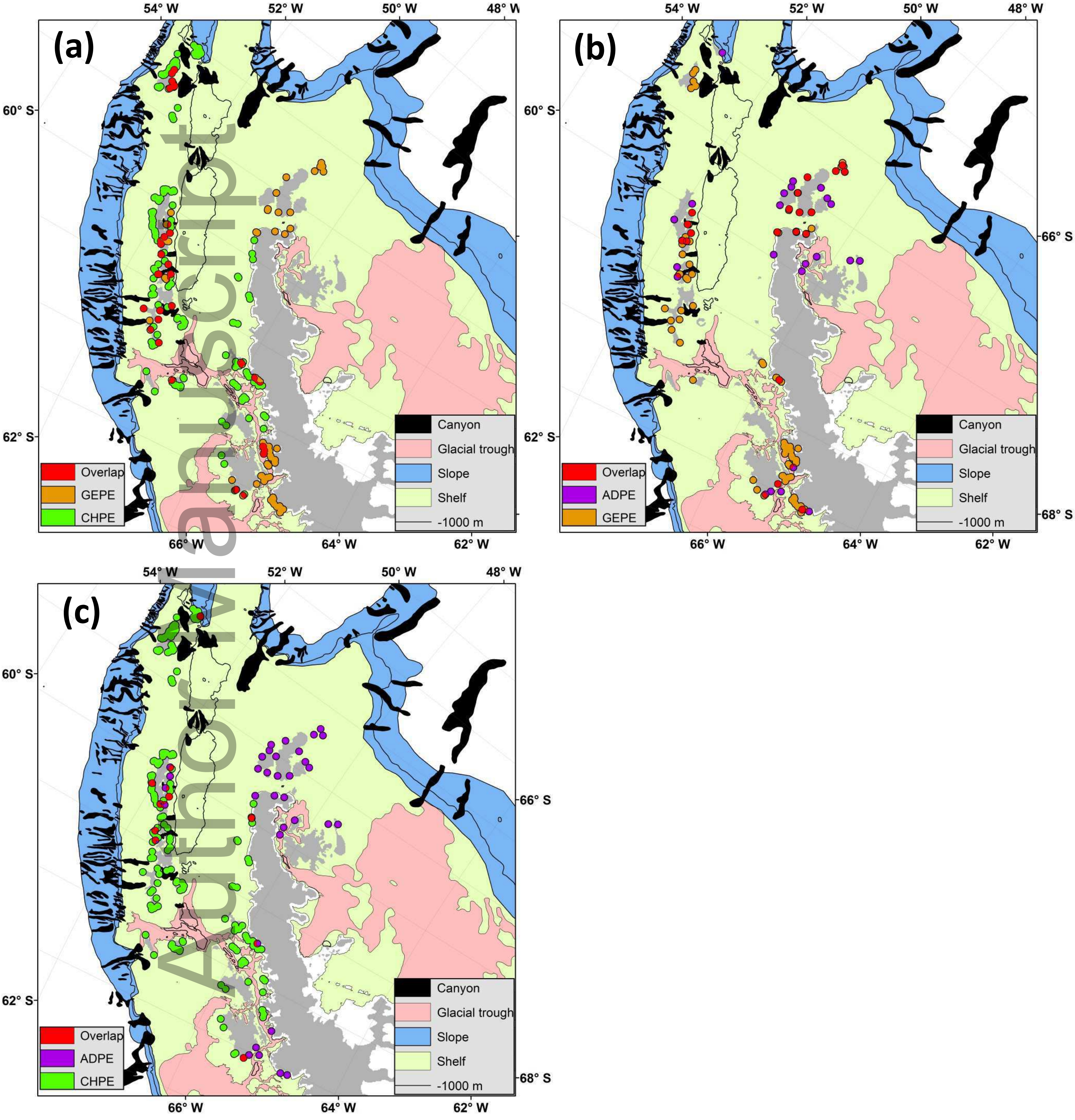

(a)
Effect on colony size
0.4
0.2
0.0
-0.2
0
50000
100000
150000
Nearest colony size
(b)
Effect on colony size
2
0
-2
-4
0
100
200
300
400
500
600
700
Distance to nearest colony (km)
(c)
Effect on colony size
1.5
1.0
0.5
0.0
-0.5
0
100
200
300
400
500
Distance to canyon (km)
(d)
Effect on colony size
0
-2
-4
-6
0
50
100
150
200
250
Distance to polynya (km)

Figure 6


(a)
(b)
(c)
54° W
52° W
50° W
48° W
60° S
62° S
66° S
68° S
66° W
64° W
62° W
Canyon
Glacial trough
Slope
Shelf
-1000 m
Overlap
GEPE
CHPE
ADPE