

Climate change and the threat of novel marine predators in Antarctica

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Abstract. Historically low temperatures have severely limited skeleton-breaking predation on the Antarctic shelf, facilitating the evolution of a benthic fauna poorly defended against durophagy. Now, rapid warming of the Southern Ocean is restructuring Antarctic marine ecosystems as conditions become favorable for range expansions. Populations of the lithodid crab *Paralomis birsteini* currently inhabit some areas of the continental slope off Antarctica. They could potentially expand along the slope and upward to the outer continental shelf, where temperatures are no longer prohibitively low. We identified two sites inhabited by different densities of lithodids in the slope environment along the western Antarctic Peninsula. Analysis of the gut contents of *P. birsteini* trapped on the slope revealed them to be opportunistic invertivores. The abundances of three commonly eaten, eurybathic taxa—ophiuroids, echinoids, and gastropods—were negatively associated with *P. birsteini* off Marguerite Bay, where lithodid densities averaged 4280 ind/km² at depths of 1100–1499 m (range 3440–5010 ind/km²), but not off Anvers Island, where lithodid densities were lower, averaging 2060 ind/km² at these depths (range 660–3270 ind/km²). Higher abundances of lithodids appear to exert a negative effect on invertebrate distribution on the slope. Lateral or vertical range expansions of *P. birsteini* at sufficient densities could substantially reduce populations of their benthic prey off Antarctica, potentially exacerbating the direct impacts of rising temperatures on the distribution and diversity of the contemporary shelf benthos.

Key words: Antarctica; bathyal; benthic; climate change; Echinoidea; Lithodidae; Ophiuroidea; *Paralomis*; polar emergence; predation.

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INTRODUCTION

Climate change is drastically altering marine ecosystems globally (Blois et al. 2013, Norris et al. 2013, Poloczanska et al. 2013). Biological invasions, range shifts, and local extirpations are occurring at an increasing rate, changing the composition of marine communities and the food webs they support (Molinis et al. 2015, Poloczanska et al. 2016, Pecl et al. 2017). As is the case for many ecosystems worldwide, climate change and its collateral effects constitute the primary threat to the persistence of contemporary, polar-marine communities (Aronson et al. 2011, 2015a, Bennett et al. 2015, Griffiths et al. 2017). Benthic ectotherms in Antarctica are particularly vulnerable to rising temperatures, because the persistently narrow range of annual sea temperatures has driven the evolution of correspondingly narrow thermal tolerances (i.e., cold-stenothermy; Pörtner 2006, Sunday et al. 2011).

Durophagous (skeleton-breaking) predators, especially decapod crustaceans, teleostean fishes, and neoselachian sharks and rays, structure benthic communities in continental-shelf environments globally, except for Antarctica. Low temperatures have prevented these predators from exerting significant control over the Antarctic-shelf benthos for millions of years, leaving asteroid, nemertean worms, and other slow-moving invertebrates as the top predators (Dayton et al. 1974, McClintock 1994, Aronson and Blake 2001, Near et al. 2012, Ortiz et al. 2017, Watson et al. 2017). Consequently, contemporary Antarctic-shelf communities are dominated by epifaunal suspension-feeders that are poorly adapted to resist durophagy (Thatje and Arntz 2004, Aronson et al. 2007). The potential for range expansion of durophagous crustaceans onto the Antarctic shelf (Aronson et al. 2015a, b) could put resident populations of invertebrates at risk, potentially exacerbating the adverse physiological and energetic effects associated with higher ambient temperatures (Barnes and Peck 2008, Deutsch et al. 2015).

King crabs (Decapoda: Anomura: Lithodidae) and other reptant (bottom-walking) decapods are broadly distributed in the deep sea and also occur in shallow waters at subpolar latitudes (Hall and Thatje 2009). Their intolerance of low temperatures (Frederich et al. 2001) has historically excluded them from the Antarctic shelf, but

climate change is now removing that barrier and conditions appear favorable for range expansion. Sea temperatures over the slope and shelf off the western Antarctic Peninsula (WAP) have risen by as much as 1.5°C over the past 50 yr (Schmidtke et al. 2014). Recently, lithodids have been recorded on the continental slope off Antarctica (Arana and Retamal 1999, García Raso et al. 2005), where they occur commonly in at least some areas (Aronson et al. 2015b, Smith et al. 2017). There appear to be no environmental barriers, thermal or otherwise, to prevent them from expanding upward onto the outer shelf (Thatje et al. 2005, Smith et al. 2012, Aronson et al. 2015b, Smith et al. 2017).

Questions remain, however, concerning the impact that lithodids have on the benthic fauna (Griffiths et al. 2013). Many lithodid species have a generalized diet consisting primarily of invertebrates (Comoglio and Amin 1999, Boudreau and Worm 2012), although little is known about the feeding habits of Antarctic lithodids. A large population of durophagous invertivores could reduce invertebrate populations in Antarctica (cf. Falk-Petersen et al. 2011); however, if the Antarctic lithodids are primarily carrion-feeders, as has been suggested (Griffiths et al. 2013, see also Smith et al. 2014), they would not have the same impact.

Paralomis birsteini is the most commonly recorded lithodid on the Antarctic slope south of 60° S (Thatje et al. 2005, 2008, Aronson et al. 2007), forming viable populations off the WAP with maximal densities in a depth range of 1100–1500 m (Aronson et al. 2015b). We located two sites along the WAP inhabited by different densities of lithodids. We then analyzed the gut contents of *P. birsteini* that we trapped on the slope and identified the primary constituents of their diet to be benthic invertebrates. Images of the benthos captured by SeaSled, a towed camera-vehicle, were used to compare the abundances and depth distributions of *P. birsteini* and their prey at each site. We compared the depth profiles of key environmental variables—sedimentary composition, temperature, and salinity—between the two sites to determine whether these physical factors could account for any differences in the distributions of the lithodids or their prey. Finally, we use these data to project the potential ecological impacts of lateral or bathymetric range expansions of the king-crab populations.

METHODS

Study sites

Benthic surveys were conducted during three oceanographic cruises—in 2010, 2013, and 2015—within two 100 × 100 km study sites spanning the outer continental shelf and slope (Fig. 1a): Marguerite Bay (MB), centered at 66°42' S, 72°12' W; and Anvers Island (AI), 380 km away and centered at 64°05' S, 66°50' W. The surveys covered a depth range of 385–2285 m, but we focused on depths of 600–1499 m, from near the shelf break at ~500 m depth to the mid-slope. This depth range included the depths of maximum density of *Paralomis birsteini* (1100–1499 m) to 500 m shallower.

The objectives of the study were threefold. First, we sought to determine the diet of lithodids

living on the continental slope off the WAP. Our second goal was to examine the relationships between lithodid density and the distribution of prey within different sites along the WAP. Third, we compared prey densities along the mid-slope with densities on the upper slope, where lithodids are not present in high densities. The intention behind this third objective was to determine whether abundances of prey on the upper slope were sufficient to support comparable densities of lithodids in the event of a range expansion.

Dietary analysis

In 2015, we collected *P. birsteini* from the slope off MB (Fig. 1b). One to three strings of six Chilean crab pots were positioned in depths ranging from 1200 to 1400 m in each of six deployments.

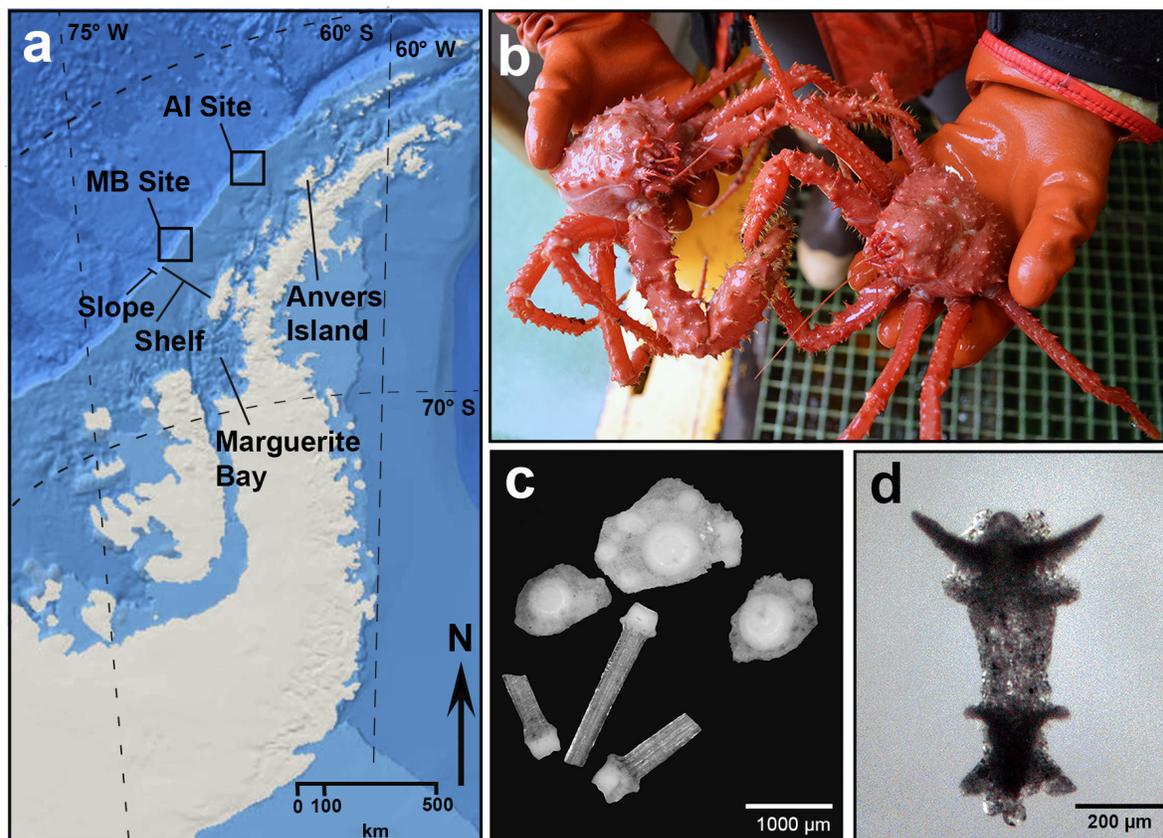


Fig. 1. Study sites, crab trapping, and gut-content analysis. (a) Location of study sites along the western Antarctic Peninsula. Constructed in ArcGIS. (b) Two *Paralomis birsteini* trapped on the upper continental slope off Marguerite Bay (MB). Carapace length of each is ~70 mm. (c) Echinoid ossicles and spines, and (d) vertebral ossicle of an ophiuroid, from the gut contents of *P. birsteini*.

The crab pots were each 142 cm in diameter and separated by 40 m of line. They were baited with sardines (*Sardinops sagax*) and deployed for approximately 32 h. Thirty *P. birsteini* (carapace length 51–82 mm) recovered in the pots were used for gut-content analysis. A Blake trawl was towed at MB to gather invertebrates from ~1150 m depth for reference. All material was frozen at -20°C for later analysis.

The foregut and hindgut of each crab were dissected under a stereomicroscope. All calcareous and chitinous parts were identified to major taxonomic group. Identifications were confirmed by comparing the parts with the invertebrates collected by trawling. The gut contents of each lithodid were scored for the presence of taxa rather than for abundance, because the prey were highly fragmented. Gut-content data were expressed as frequencies of occurrence in the sample of *P. birsteini*, with the goal of identifying which invertebrates the lithodids were consuming.

Seafloor-imaging study

Thirty-five transects—23 at MB and 12 at AI—averaging 8 km in length, spanning 600–1499 m, and covering a total area of 298,999 m², were digitally imaged using the towed camera-vehicle SeaSled, owned and operated by the Woods Hole Oceanographic Institution, Woods Hole, Massachusetts, USA (see Appendix S1: Table S1 for specifications of SeaSled during the three cruises and Appendix S1: Table S2 for details of the transects). The starting points of the transects were determined using a stratified-random sampling design. The number of transects sampled in each depth stratum was the maximum feasible given the constraints of ship-time, weather, and equipment in Antarctica. Paired, slightly overlapping images were collected along each transect by two cameras mounted side by side, yielding 96,786 usable images captured from altitudes of 0.5–4.0 m above the seafloor. All images captured from altitudes >4.0 m were discarded because image clarity diminished with height above the seafloor. Both images from each pair were used for data collected in 2010 and 2013. In 2015, image clarity was reduced in one camera, so only images from the other camera were used.

To compare the diet of *P. birsteini* with the availability of food resources in the environment, we examined the distributional patterns of the

lithodids and the four epifaunal prey taxa most commonly identified within both the gut contents and the seafloor images. Depth distributions of *P. birsteini*, ophiuroids, echinoids, gastropods, and asteroids were determined from the images. *P. birsteini* could be counted accurately in images taken at ≤ 4 m altitude, although they were sometimes visible in images from higher altitudes. The prey taxa, which were typically smaller than *P. birsteini*, were clearly visible in images taken at ≤ 3 m altitude. All four prey taxa are broadly distributed across shelf and slope depths in Antarctica (Clarke et al. 2004) and were clearly visible in our images. Of the mollusks, we only analyzed gastropods. Most of the bivalve taxa are infaunal and, therefore, were not evident in the images.

The population density and depth distribution of *P. birsteini* were estimated for each site by assigning all usable images to 100-m depth bins. For each transect, the number of *P. birsteini* within a depth bin was divided by the total area covered by usable images within the depth bin. Within a transect, only depth bins with ≥ 200 m² of usable images were included. The area covered by each image was determined trigonometrically from its dimensions and altitude (Aronson et al. 2015b). The total area was corrected for overlap between image pairs and between successive images. Densities were averaged for all transects within a depth bin at each site to give a mean density of crabs per 1000 m². Because *P. birsteini* were rare in the images, 95% confidence intervals were calculated for each depth bin assuming a Poisson distribution.

Prey taxa were more abundant in the images than *P. birsteini*. For each depth bin in each study site, the densities and depth distributions of prey were estimated using 200 images randomly selected from the usable images from all transects. Exceptions were made for four depth bins for which fewer than 200 images were available: At MB, 132 images were available at 1400–1499 m; and at AI, 172, 46, and 96 images were available at 500–599, 600–699, and 1100–1199 m, respectively. Because prey taxa were common in the images, 95% confidence intervals were calculated assuming those taxa were normally distributed within depth bins. Images collected during 2010 and 2013 were used in this analysis; images from 2015 lacked sufficient definition to count prey taxa reliably.

Environmental variables

At each site, temperature and salinity were estimated for every 50-m depth mark by averaging all data recorded by the CTD aboard SeaSled within ± 10 m of the depth mark, at an altitude of 1–4 m above the seafloor (see Appendix S1: Table S1 for CTD specifications). The substrate composition was determined for each site using 100 randomly selected images per depth bin captured at a maximum altitude of 3 m (except for 600–699 and 1100–1199 m at AI, where 46 and 96 images were available). Using Coral Point Count with Excel extensions (Kohler and Gill 2006), five points were randomly placed on each image within a 58×58 cm plot superimposed on each image. The grain of sediment directly beneath each point was measured along its longest axis and classified by size. Four standard categories were used: fine-grained sediment (<4 mm), pebble (4 to <64 mm), cobble (64 to <256 mm), and boulder (≥ 256 mm).

Statistical analysis of depth distributions

Depth distributions of each taxon were compared between sites using the Kolmogorov–Smirnov (K–S) two-sample test (coded in Matlab after Zar 1999 and Roth et al. 2010). Paired t tests were used to compare the densities of each taxon between sites (coded in R; R Core Development Team 2008). Separately, paired t tests were used to compare the densities of prey taxa on the upper slope (600–999 m), where lithodids were rare or absent. The relationships between densities of *P. birsteini* and each prey taxon were examined within sites using regression analysis employing an exponential model. For multiple independent tests, the Holm–Bonferroni correction was used to maintain an overall type I error rate, α , of 0.05. The correction provides a running adjustment of α (Holm 1979). The P -values for the individual tests are presented with their corresponding adjusted rates, α_{adj} .

Variations in sedimentary composition with depth were compared between sites using a nested analysis of similarity (ANOSIM), in which depth was nested within site. The ANOSIM was run using the PRIMER v6 software package (Clarke and Gorley 2006). Depth profiles of temperature and salinity were compared between sites using paired t tests, coded in R (R Core Development Team 2008).

RESULTS

Dietary analysis

Prey items were identified in the gut contents of 27 of the 30 *Paralomis birsteini* examined. The most prevalent prey were ophiuroids, which we found in 78% of the lithodids containing prey, followed by mollusks (gastropods and bivalves) and echinoids (Figs. 1c, d, 2). Asteroids, holothuroids, polychaetes, bryozoans, and poriferans were also identified in the gut contents. Between 1 and 5 major macrofaunal taxa were found in each crab (mean 2.5). Fish and amphipods were frequently observed in the gut contents. Fish were used to bait the crab traps and the bait attracted amphipods in large numbers. Because the prevalence of these two categories in gut samples was likely a consequence of the trapping procedure, they were excluded from further analysis. No other taxa were recovered in the crab traps. The observation of bait in the gut contents of *P. birsteini* and a previous observation of them feeding on a whale-fall off AI (Smith et al. 2014) do, however, indicate that they opportunistically consume carrion.

Seafloor-imaging study

Using 96,786 images captured by SeaSled, we examined the depth distributions of *P. birsteini* and the four prey taxa—ophiuroids, echinoids, gastropods, and asteroids—at both sites. *P. birsteini* were observed in the images at minimum depths

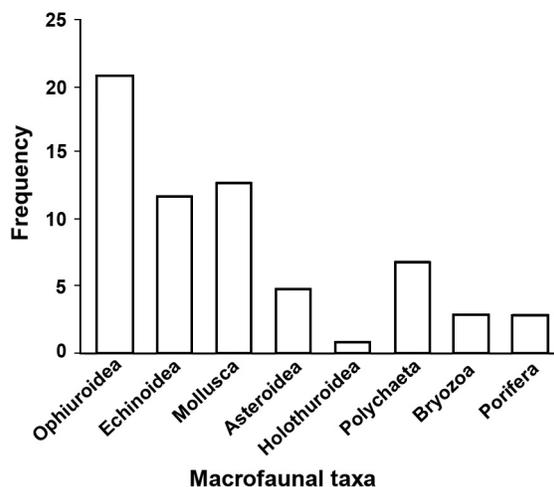


Fig. 2. Frequencies of occurrence of macrofaunal invertebrates identified in the gut contents of 27 *Paralomis birsteini*.

of 721 m at MB and 866 m at AI. After discarding the images from altitudes >4 m, the shallowest records of *P. birsteini* in the analysis were 841 and 933 m, respectively (Appendix S1: Table S3). Most *P. birsteini* were observed at mid-slope depths, within a range of 1100–1499 m (Fig. 3a, b). A small number of a second lithodid species, *Neolithodes yaldwyni*—fewer than 10 individuals at the two sites combined—were observed across these depths and were omitted from analysis. The depth distributions of *P. birsteini* were not significantly different at the two sites (Kolmogorov–Smirnov [K–S] test: $D = 0.209$, $n_{AI} = 7$, $n_{MB} = 7$, $P = 0.522$). Crab density was, however, significantly higher at MB than at AI (two-tailed, paired t test: $t = 3.578$, $df = 6$, $P = 0.012$). Over the depth range of 1100–1499 m, *P. birsteini* averaged 4280 ind/km² at MB and 2060 ind/km² at AI (ranges 3440–5010 and 660–3270 ind/km², respectively).

Identifications of prey below the level of class were generally not feasible in either the gut contents or the images. Even at this coarse level, however, our analysis revealed striking patterns of prey distribution with respect to the distribution of their predators. Differences in lithodid densities between MB and AI were associated with disparities in the distributions or densities of the invertebrate taxa most commonly identified in the gut contents.

The density distributions across depth bins of ophiuroids and echinoids—both of which were commonly identified in gut contents—were significantly different between the two study sites (K–S tests for ophiuroids and echinoids, respectively: $D = 0.374$, $P = 0.0005$, $\alpha_{adj} = 0.0167$; and $D = 0.609$, $P < 0.0001$, $n_{AI} = 9$, $n_{MB} = 9$ in both cases; $\alpha_{adj} = 0.0125$). At MB, both taxa were more concentrated in shallow-slope depths and low, roughly comparable densities inhabited depths overlapping the peak distribution of lithodids. In contrast, at AI, where the lithodids were less abundant, the depth distribution of ophiuroids was more uniform across depths and echinoids were more common across mid-slope depths (Fig. 3c–f). Overall densities of ophiuroids and echinoids were not significantly different between MB and AI (one-tailed, paired t tests for MB and AI, respectively: $t = 0.222$, $df = 8$, $P = 0.415$; and $t = 2.201$, $df = 8$, $P = 0.039$; $\alpha_{adj} = 0.0167$ in both cases). Gastropods, which were also common in the lithodids guts, showed a different pattern:

There was no significant difference in depth distribution between MB and AI (K–S test: $D = 0.226$, $n_{AI} = 9$, $n_{MB} = 9$, $P = 0.385$, $\alpha_{adj} = 0.025$), but there were significantly more gastropods at AI (one-tailed, paired t test: $t = 8.50$, $df = 8$, $P < 0.0001$, $\alpha_{adj} = 0.0125$; Fig. 3g, h).

The relationships between the depth distributions of *P. birsteini* and these three taxa were confirmed using regression analysis. Significant, negative-exponential relationships were observed at MB between lithodids and ophiuroids ($r^2 = 0.649$, $P = 0.009$), lithodids and echinoids ($r^2 = 0.651$, $P = 0.009$), and lithodids and gastropods ($r^2 = 0.712$, $P = 0.004$; $N = 9$, $\alpha_{adj} = 0.0125$ in all three cases). These relationships were not significant at AI ($r^2 = 0.018$, $P = 0.731$; $r^2 = 0.016$, $P = 0.744$; and $r^2 = 0.522$, $P = 0.028$, respectively; $N = 9$, $\alpha_{adj} = 0.0125$ in all three cases).

Asteroid fragments were rarely identified in gut contents compared with the other three taxa (Fig. 3i, j). There was no difference in either the densities (two-tailed, paired t test: $t = 2.169$, $df = 8$, $P = 0.062$, $\alpha_{adj} = 0.0167$) or depth distributions (K–S test: $D = 0.292$, $n_{AI} = 9$, $n_{MB} = 9$, $P = 0.052$, $\alpha_{adj} = 0.025$; Fig. 3i, j) of asteroids between sites. A significant, negative relationship was, however, observed between lithodids and asteroids at MB ($r^2 = 0.579$, $N = 9$, $P = 0.017$, $\alpha_{adj} = 0.05$). No relationship was detected between the two taxa at AI ($r^2 = 0.266$, $N = 9$, $P = 0.155$; $\alpha_{adj} = 0.0125$).

Prey densities on the upper slope were broadly comparable between MB and AI. Paired t tests detected no significant differences in the densities of ophiuroids, echinoids, or asteroids between the two sites at 600–999 m (two-tailed, paired t tests for the three prey taxa, respectively: $t = 2.623$, $P = 0.079$; $t = 0.404$, $P = 0.713$; and $t = 1.319$, $P = 0.279$; $df = 3$, $\alpha_{adj} = 0.0167$ in all three cases), although more gastropods were observed in this depth range at AI ($t = 5.870$, $df = 3$, $P = 0.010$; $\alpha_{adj} = 0.0125$).

Physical parameters

Comparison of the sedimentary composition between the two sites revealed no significant differences in observed frequencies of sedimentary size classes on the seafloor (nested ANOSIM: $R = 0.088$, $N = 18$, $P = 0.11$; Fig. 4a, b). We also found no differences in either temperature or salinity profiles between the two sites (two-tailed,

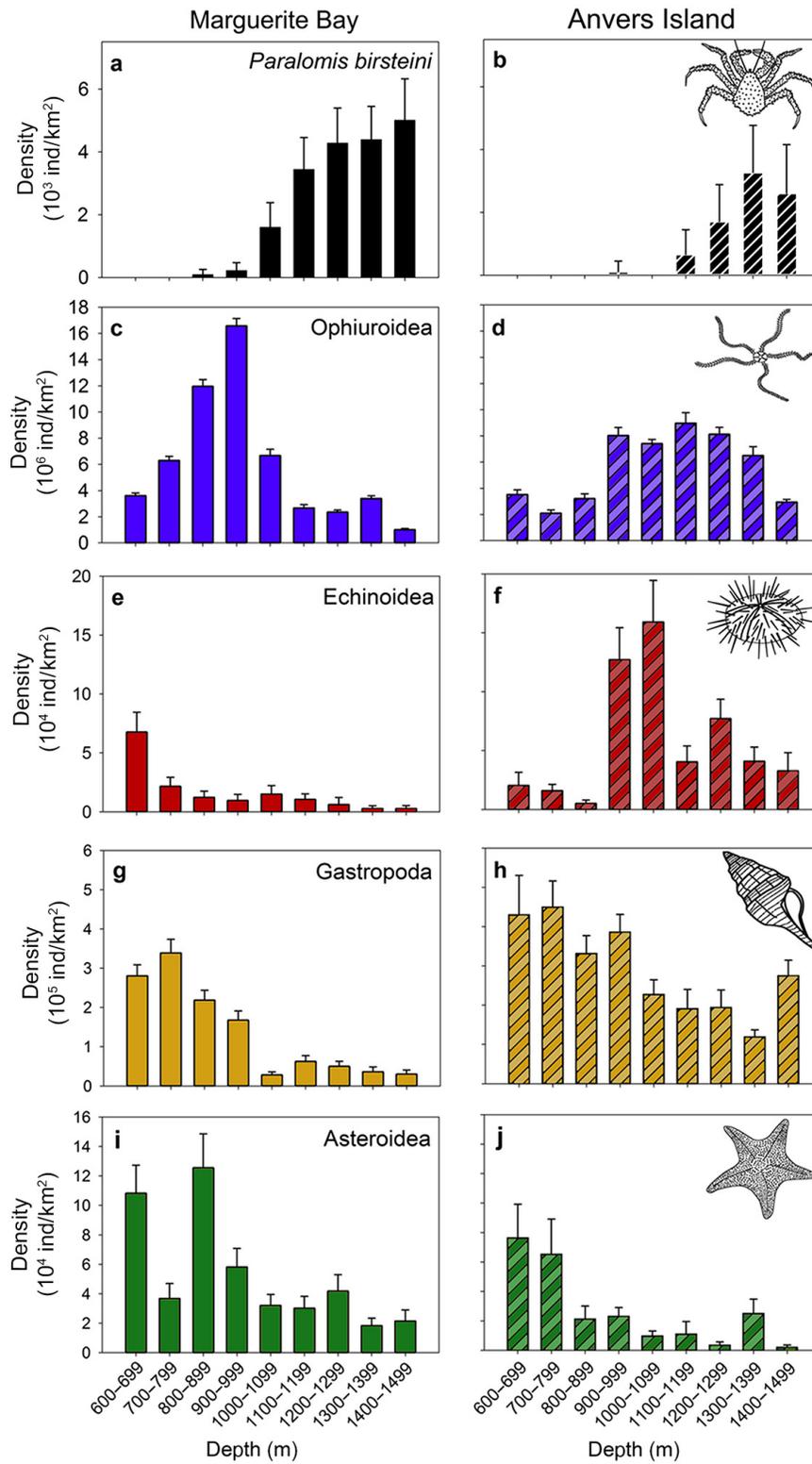


Fig. 3. Density distributions of *Paralomis birsteini* and prey taxa off the western Antarctic Peninsula. (a–j) Plots

(Fig. 3. Continued)

in the left column show data from Marguerite Bay (MB), and plots in the right column show data from Anvers Island. Population densities of all taxa are scaled to numbers of individuals per km². Error bars represent upper 95% confidence intervals. For *P. birsteini*, confidence intervals were calculated assuming the data are Poisson-distributed within each depth bin. For the prey taxa, confidence intervals were calculated assuming the data are normally distributed within each depth bin. Data on prey distributions from MB are from Aronson et al. (2015b).

paired *t* tests: $t = 1.633$, $df = 18$, $P = 0.11$; and $t = 0.046$, $df = 18$, $P = 0.96$; Fig. 5a, b).

DISCUSSION

Our data support the hypothesis that when and where *Paralomis birsteini* are sufficiently abundant,

they negatively impact their macrofaunal prey on the Antarctic slope. At MB, densities of the lithodids at 1100–1499 m depth were negatively associated with prey densities. Common prey taxa were consistently observed at lower densities across this depth range at MB, compared with the same depth range at AI, where the lithodids were less abundant. In contrast, the pattern of abundance of asteroids, which were less common in the gut contents, was similar at both sites. Other predators, including skeleton-breaking teleosts and elasmobranchs, as well as cephalopods, were rare or absent within our study sites (Targett 1981, Daniels 1982, Long 1994, Eastman et al. 2013, Amsler et al. 2016), leaving lithodids as the only ecologically significant durophagous predators. Lithodids themselves have few or no predators in this region (Bansode et al. 2014, Aronson et al. 2015b).

Like other lithodid species, *P. birsteini* feeds on a broad range of invertebrates (Comoglio and Amin 1999, Boudreau and Worm 2012). The patterns in species distribution reported in the present study are likely to differ at other locations with varying predator abundance and prey availability. For example, in Palmer Deep, a 1440-m-deep basin on the continental shelf off the WAP, *Neolithodes yaldwyni* were reported at densities of 10,600 km⁻² (Smith et al. 2012). At the depths inhabited by *N. yaldwyni* (<850 m), echinoderms were completely absent and the diversity of other epibenthic megafauna was low. In shallower depths within Palmer Deep where *N. yaldwyni* were absent, echinoderms were abundant and epifaunal diversity was higher. Smith et al. (2012) hypothesized that the break in lithodid–echinoderm distribution was driven by predation. In the Barents Sea, introduced lithodids, *Paralithodes camtschaticus*, have radically altered the structure and function of benthic communities in some areas (Falk-Petersen et al. 2011, Oug et al. 2017). In Antarctica, imaging and trapping studies at additional locations along the slope will provide a fuller picture of the contemporary

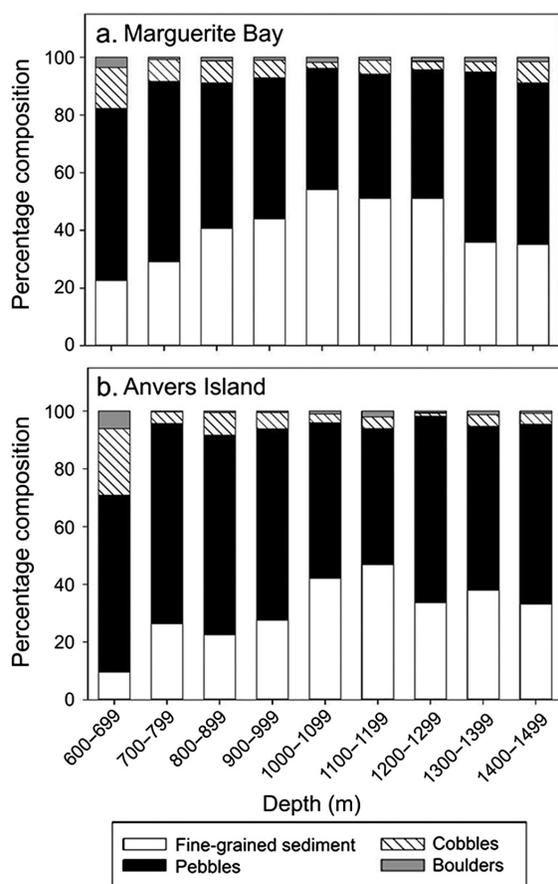


Fig. 4. Sedimentary composition with depth at two sites along the western Antarctic Peninsula. (a) Marguerite Bay (MB) and (b) Anvers Island (AI). Frequency data were converted to percentages for ease of interpretation ($n = 4500$ points analyzed in images from MB; $n = 4210$ from AI).

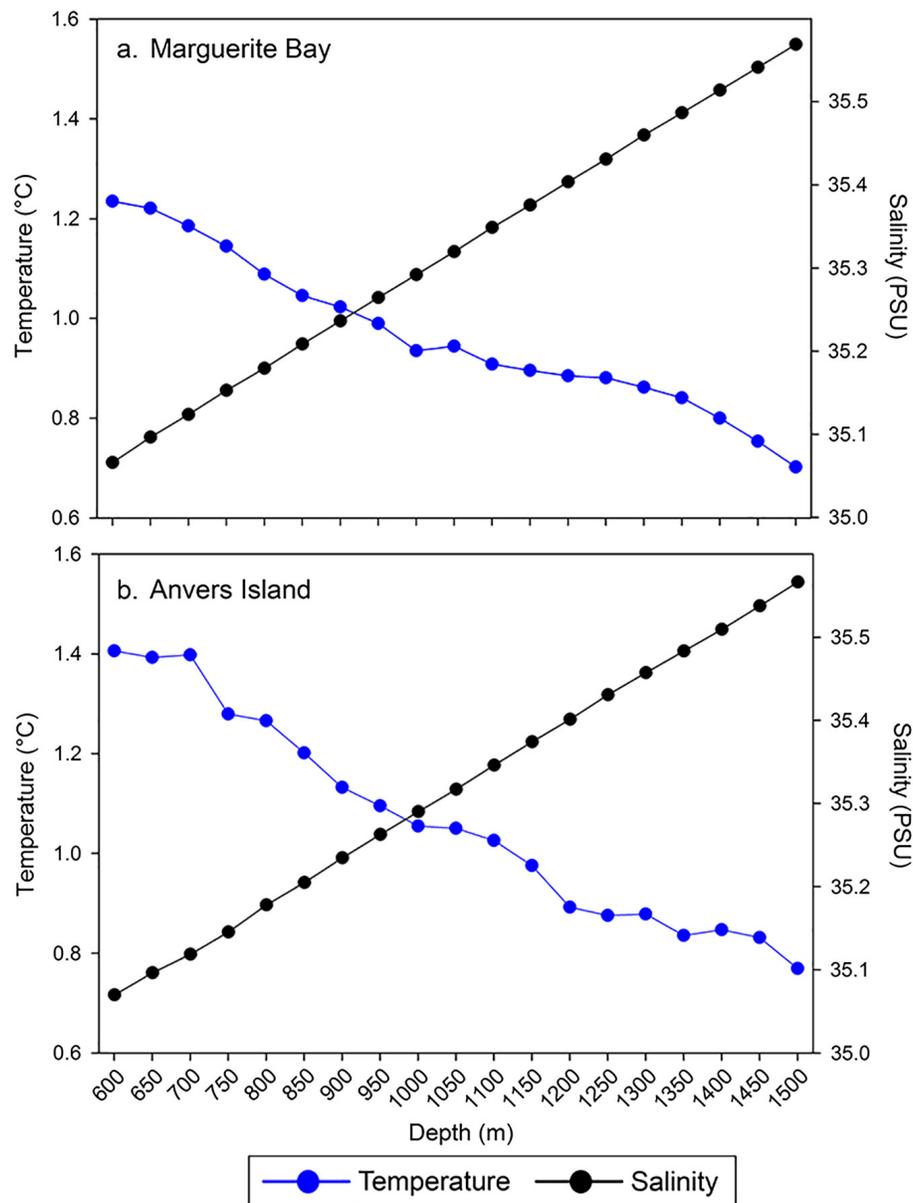


Fig. 5. Depth profiles of temperature and salinity at two sites along the western Antarctic Peninsula. (a) Marguerite Bay and (b) Anvers Island. Each point represents averaged CTD data collected from within ± 10 m of the depth mark at an altitude of 1–4 m above the seafloor. For each point, the standard error was ≤ 0.007 ; consequently, standard error bars would not be visible on the plots and are not included.

ecological effects of durophagous predation on the slope and potential effects on the shelf. Based on the evidence presented by us and others (e.g., Falk-Petersen et al. 2011, Smith et al. 2012), range expansions of *P. birsteinii* could restructure the shelf benthos off the WAP.

Temperature, salinity, and sedimentary composition were comparable between sites. These similarities suggest that none of the three environmental variables are likely to account for the disparities in the population densities or depth distributions of the lithodids or their prey. Either

other sources of natural variability, such as hydrography or primary production, are responsible for the difference in density of *P. birsteini* between the sites, or the lithodids colonized AI more recently.

Deployment of three HOBO U12–015 temperature loggers off AI at 411–430 m depth, at an altitude of 3 m above the bottom from February 2015 to February 2016, revealed an annual range of sea temperatures on the shelf of 1.0–1.8°C. That range falls within the thermal tolerance of *P. birsteini* (–0.4–2.5°C) and other lithodid species occurring off the WAP (Hall and Thatje 2011). At MB, Aronson et al. (2015b) reported summer shelf temperatures in the range of 1.2–1.6°C at 400 m. Considering the similarity in upper- and mid-slope seafloor temperatures at MB and AI, shelf temperatures at MB can be expected to fall within a similar annual range.

At no time of year should water temperature impede the survival of lithodids on the outer shelf at either location. The higher abundances of prey on the upper slope (600–999 m) and shallower (Aronson et al. 2015b) indicate that food resources are also unlikely to limit the expansion of *P. birsteini* into shallower water. Increasing water temperatures are unlikely to thermally limit the distribution of either lithodids or their prey; Antarctic benthic invertebrates living at the temperatures within the range found on the shelf today are typically capable of surviving at higher temperatures (Griffiths et al. 2017).

Waters off the WAP continue to warm at an unprecedented rate (Schmidtko et al. 2014, DeConto and Pollard 2016), decreasing the probability of negative thermal anomalies and increasing the likelihood that reptant decapods on the Antarctic slope will expand their ranges (Hall and Thatje 2009). Warming in this region has been linked to the potential for range expansions of other taxa (Aronson et al. 2007, Barnes and Peck 2008, Molinos et al. 2015, but see Griffiths et al. 2017), including the predatory asteroid *Asterias amurensis* (Byrne et al. 2016). The benthic faunas of the upper slope and shelf are poorly defended against durophagous predation (Watson et al. 2017). Prey densities on the upper slope, combined with the generalized diet of *P. birsteini*, strongly suggest that comparable populations of lithodids could be supported in that environment at both sites.

Durophagous predators have not been ecologically significant components of the food webs of shelf habitats in Antarctica for millions of years. The emergence of lithodids into these naïve ecological settings in Antarctica could have far-reaching implications for the seafloor ecosystems by exacerbating the direct, physiological effects of rising temperatures on community structure and function. As water temperatures over the shelf continue to rise, benthic habitats closer to shore will become increasingly suitable for durophagous predators. Lithodids and other durophagous predators (Aronson et al. 2007, 2015a) have the potential to return, draw down populations of benthic invertebrates, and thereby compromise the existing character of the contemporary benthic communities. The result would be structural and functional homogenization of the Antarctic bottom fauna with temperate and tropical faunas around the world.

Ecological studies of the deep sea, especially in an area as remote as the WAP, are limited by the high cost and logistical difficulty of collecting statistically robust ecological data. Assembling our dataset from two locations required three oceanographic cruises over a five-year period. The patterns are revealing, and although there could be other factors interacting with predation, our results represent an important step toward projecting the impacts of lithodids on the upper slope and outer shelf off the western Antarctic Peninsula. Imaging and trapping studies at other locations along the Antarctic slope will provide a fuller picture of the ecological effects of durophagous predation. Looking forward, predator–prey dynamics in Antarctica will reflect the interplay of the physical, chemical, and biological effects of climate change. The hypothesis of increasing durophagous predation will be tested by long-term observation on a broad geographic scale.

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LITERATURE CITED

- Amsler, M. O., J. T. Eastman, K. E. Smith, J. B. McClintock, H. Singh, S. Thatje, and R. B. Aronson. 2016. Zonation of demersal fishes off Anvers Island, western Antarctic Peninsula. *Antarctic Science* 28: 44–50.
- Arana, P. M., and M. A. Retamal. 1999. Nueva distribución de *Paralomis birsteini* Macpherson, 1988 en aguas antárticas (Anomura, Lithodidae, Lithodinae). *Investigaciones Marinas, Valparaíso* 27:101–110.
- Aronson, R. B., and D. B. Blake. 2001. Global climate change and the origin of modern benthic communities in Antarctica. *American Zoologist* 41:27–39.
- Aronson, R. B., M. Frederich, R. Price, and S. Thatje. 2015a. Prospects for the return of shell-crushing crabs to Antarctica. *Journal of Biogeography* 42:1–7.
- Aronson, R. B., et al. 2015b. No barrier to emergence of bathyal king crabs on the Antarctic shelf. *Proceedings of the National Academy of Sciences USA* 122:12997–13002.
- Aronson, R. B., S. Thatje, A. Clarke, L. S. Peck, D. B. Blake, C. D. Wigla, and B. A. Seibel. 2007. Climate change and invasibility of the Antarctic benthos. *Annual Review of Ecology, Evolution and Systematics* 38:129–154.
- Aronson, R. B., S. Thatje, J. B. McClintock, and K. A. Hughes. 2011. Anthropogenic impacts on marine ecosystems in Antarctica. *Annals of the New York Academy of Sciences* 1223:82–107.
- Bansode, M. A., J. T. Eastman, and R. B. Aronson. 2014. Feeding biomechanics of five demersal Antarctic fishes. *Polar Biology* 37:1835–1848.
- Barnes, D. K. A., and L. S. Peck. 2008. Vulnerability of Antarctic shelf biodiversity to predicted regional warming. *Climate Research* 37:499–504.
- Bennett, J. R., et al. 2015. Polar lessons learned: long-term management based on shared threats in Arctic and Antarctic environments. *Frontiers in Ecology and the Environment* 13:316–324.
- Blois, J. L., P. L. Zarnetske, M. C. Fitzpatrick, and S. Finnegan. 2013. Climate change and the past, present, and future of biotic interactions. *Science* 341:499–504.
- Boudreau, S. A., and B. Worm. 2012. Ecological role of large benthic decapods in marine ecosystems: a review. *Marine Ecology Progress Series* 469:195–213.
- Byrne, M., M. Gall, K. Wolfe, and A. Agüera. 2016. From pole to pole: the potential for the Arctic seastar *Asterias amurensis* to invade a warming Southern Ocean. *Global Change Biology* 22:3874–3887.
- Clarke, A., R. B. Aronson, J. A. Crame, J.-M. Gili, and D. B. Blake. 2004. Evolution and diversity of the benthic fauna of the Southern Ocean continental shelf. *Antarctic Science* 16:559–568.
- Clarke, K. R., and R. N. Gorley. 2006. PRIMER v6: user manual/tutorial. PRIMER-E, Plymouth Marine Laboratory, Plymouth, UK.
- Comoglio, L. I., and O. A. Amin. 1999. Feeding habits of the false southern king crab *Paralomis granulosa* (Lithodidae) in the Beagle Channel, Tierra del Fuego, Argentina. *Scientia Marina* 63(Suppl 1):361–366.
- Daniels, R. A. 1982. Feeding ecology of some fishes of the Antarctic Peninsula. *Fishery Bulletin* 80: 575–588.
- Dayton, P. K., G. A. Robilliard, R. T. Paine, and L. B. Dayton. 1974. Biological accommodation in the benthic community at McMurdo Sound, Antarctica. *Ecological Monographs* 44:105–128.
- DeConto, R. M., and D. Pollard. 2016. Contributions of Antarctica to past and future sea-level rise. *Nature* 531:591–597.
- Deutsch, C., A. Ferrel, B. Seibel, H.-O. Pörtner, and R. B. Huey. 2015. Climate change tightens a metabolic constraint on marine habitats. *Science* 348:1132–1135.
- Eastman, J. T., M. O. Amsler, R. B. Aronson, S. Thatje, J. B. McClintock, S. C. Vos, J. W. Kaeli, H. Singh, and M. La Mesa. 2013. Photographic survey of benthos provides insights into the Antarctic fish fauna from the Marguerite Bay slope and the Amundsen Sea. *Antarctic Science* 25:31–43.
- Falk-Petersen, J., P. Renaud, and N. Anisimova. 2011. Establishment and ecosystem effects of the alien invasive red king crab (*Paralithodes camtschaticus*) in the Barents Sea: a review. *ICES Journal of Marine Science* 68:479–488.
- Frederich, M., F. J. Sartoris, and H. O. Pörtner. 2001. Distribution patterns of decapod crustaceans in polar areas: A result of magnesium regulation? *Polar Biology* 24:719–723.
- García Raso, J. E., M. E. Manjón-Cabez, A. Ramos, and I. Olasi. 2005. New record of Lithodidae (Crustacea, Decapoda, Anomura) from the Antarctic (Bellingshausen Sea). *Polar Biology* 28:642–646.

- Griffiths, H. J., A. J. Meijers, and T. J. Bracegirdle. 2017. More losers than winners in a century of future Southern Ocean seafloor warming. *Nature Climate Change* 7:749–754.
- Griffiths, H. J., R. J. Whittle, S. J. Roberts, M. Belchier, and K. Linse. 2013. Antarctic crabs: Invasion or endurance? *PLoS ONE* 8:e66981.
- Hall, S., and S. Thatje. 2009. Global bottlenecks in the distribution of marine Crustacea: temperature constraints in the family Lithodidae. *Journal of Biogeography* 36:2125–2135.
- Hall, S., and S. Thatje. 2011. Temperature-driven biogeography of the deep-sea family Lithodidae (Crustacea: Decapoda: Anomura) in the Southern Ocean. *Polar Biology* 34:363–370.
- Holm, S. 1979. A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics* 6:65–70.
- Kohler, K. E., and S. M. Gill. 2006. Coral point count with Excel extensions (CPCe): a visual basic program for the determination of coral and substrate coverage using random point count methodology. *Computers and Geosciences* 32:1259–1269.
- Long, D. J. 1994. Colonization or Paleogene persistence? Historical biogeography of skates (Chondrichthyes: Rajidae) in the Antarctic ichthyofauna. *Paleobiology* 20:215–228.
- McClintock, J. B. 1994. The trophic biology of Antarctic shallow-water echinoderms. *Marine Ecology Progress Series* 111:191–202.
- Molinos, J. G., B. S. Halpern, D. S. Schoeman, C. J. Brown, W. Kiessling, P. J. Moore, J. M. Pandolfi, E. S. Poloczanska, A. J. Richardson, and M. T. Burrows. 2015. Climate velocity and the future global redistribution of marine biodiversity. *Nature Climate Change* 6:83–88.
- Near, T. J., A. Dornburg, K. L. Kuhn, J. T. Eastman, J. N. Pennington, T. Patarnello, L. Zane, D. A. Fernández, and C. D. Jones. 2012. Ancient climate change, antifreeze, and the evolutionary diversification of Antarctic fishes. *Proceedings of the National Academy of Sciences USA* 109:3434–3439.
- Norris, R. D., S. K. Turner, P. M. Hull, and A. Ridgwell. 2013. Marine ecosystem responses to Cenozoic global change. *Science* 341:492–498.
- Ortiz, M., B. Hermosillo-Nuñez, J. González, F. Rodríguez-Zaragoza, I. Gómez, and F. Jordán. 2017. Quantifying keystone species complexes: ecosystem-based conservation management in the King George Island (Antarctic Peninsula). *Ecological Indicators* 81:453–460.
- Oug, E., J. H. Sundet, and S. K. J. Cochrane. 2017. Structural and functional changes of soft-bottom ecosystems in northern fjords invaded by the red king crab (*Paralithodes camtschaticus*). *Journal of Marine Systems*. <https://doi.org/10.1016/j.jmarsys.2017.07.005>
- Pecl, G. T., et al. 2017. Biodiversity redistribution under climate change: impacts on ecosystems and human well-being. *Science* 355:6332.
- Poloczanska, E. S., et al. 2013. Global imprint of climate change on marine life. *Nature Climate Change* 3:919–925.
- Poloczanska, E. S., et al. 2016. Responses of marine organisms to climate change across oceans. *Frontiers in Marine Science* 3:62.
- Pörtner, H. O. 2006. Climate-dependent evolution of Antarctic ectotherms: an integrative analysis. *Deep-Sea Research Part II: Topical Studies in Oceanography* 52:1071–1104.
- R Core Development Team. 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Roth, L., S. Koksal, and R. van Woesik. 2010. Effects of thermal stress on key processes driving coral-population dynamics. *Marine Ecology Progress Series* 411:73–87.
- Schmidtke, S., K. T. Heywood, A. F. Thompson, and S. Aoki. 2014. Multidecadal warming of Antarctic waters. *Science* 346:1227–1230.
- Smith, K. E., R. B. Aronson, S. Thatje, G. A. Lovrich, M. O. Amsler, B. V. Steffel, and J. B. McClintock. 2017. Biology of the king crab *Paralomis birsteini* on the continental slope off the western Antarctic Peninsula. *Polar Biology*. <https://doi.org/10.1007/s00300-017-2145-9>.
- Smith, C. R., L. J. Grange, D. L. Honig, L. Naudts, B. Huber, L. Guidi, and E. Domak. 2012. A large population of king crabs in Palmer Deep on the west Antarctic Peninsula shelf and potential invasive impacts. *Proceedings of the Royal Society B* 279:1017–1026.
- Smith, K. E., et al. 2014. Discovery of a recent, natural whale fall on the continental slope off Anvers Island, western Antarctic Peninsula. *Deep-Sea Research Part I: Oceanographic Research Papers* 90:76–80.
- Sunday, J. M., A. E. Bates, and N. K. Dulvy. 2011. Global analysis of thermal tolerance and latitude in ectotherms. *Proceedings of the Royal Society of London B: Biological Sciences* 278:1823–1830.
- Targett, T. E. 1981. Trophic ecology and structure of coastal Antarctic fish communities. *Marine Ecology Progress Series* 4:243–263.
- Thatje, S., K. Anger, J. A. Calcagno, G. A. Lovrich, H.-O. Pörtner, and W. E. Arntz. 2005. Challenging the cold: Crabs reconquer the Antarctic. *Ecology* 86:619–625.

- Thatje, S., and W. E. Arntz. 2004. Antarctic reptant decapods: More than a myth? *Polar Biology* 27: 195–201.
- Thatje, S., S. Hall, C. Hauton, C. Held, and P. Tyler. 2008. Encounter of *Paralomis birsteini* on the continental slope off Antarctica, sampled by ROV. *Polar Biology* 31:1143–1148.
- Watson, S.-A., S. A. Morley, and L. S. Peck. 2017. Latitudinal trends in shell production cost from the tropics to the poles. *Science Advances* 3: e1701362.
- Zar, J. H. 1999. *Biostatistical analysis*. Fourth edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

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