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King crabs and Antarctic shelf fauna

Mouse model of human mitochondrial disorder

Cytosolic DNA and autoimmune diseases

Urine excretion in lab-grown kidneys

Radioimmunotherapy for Hodgkin's lymphoma

No barrier to emergence of bathyal king crabs on the Antarctic shelf

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Cold-water conditions have excluded durophagous (skeleton-breaking) predators from the Antarctic seafloor for millions of years. Rapidly warming seas off the western Antarctic Peninsula could now facilitate their return to the continental shelf, with profound consequences for the endemic fauna. Among the likely first arrivals are king crabs (Lithodidae), which were discovered recently on the adjacent continental slope. During the austral summer of 2010–2011, we used underwater imagery to survey a slope-dwelling population of the lithodid *Paralomis birsteini* off Marguerite Bay, western Antarctic Peninsula for environmental or trophic impediments to shoreward expansion. The population density averaged ∼4.5 individuals × 1,000 m^{-2} within a depth range of 1,100–1,500 m (overall observed depth range 841–2,266 m). Images of juveniles, discarded molts, and precopulatory behavior, as well as gravid females in a trapping study, suggested a reproductively viable population on the slope. At the time of the survey, there was no thermal barrier to prevent the lithodids from expanding upward and emerging on the outer shelf (400- to 550-m depth); however, near-surface temperatures remained too cold for them to survive in inner-shelf and coastal environments (<200 m). Ambient salinity, composition of the substrate, and the depth distribution of potential predators likewise indicated no barriers to expansion of lithodids onto the outer shelf. Primary food resources for lithodids—echinoderms and mollusks—were abundant on the upper slope (550–800 m) and outer shelf. As sea temperatures continue to rise, lithodids will likely play an increasingly important role in the trophic structure of subtidal communities closer to shore.

biological invasion | polar emergence | climate change | predation | Southern Ocean

Climate change is substantially altering the composition and function of marine and terrestrial ecosystems (1–5). Polar-marine communities are particularly vulnerable to climate change, which at this point is the principal threat to their persistence (6). The near-absence of seasonal variation in sea temperature has led to the dominance of cold-stenothermal faunas, which have limited capacities to acclimate to rapid warming (7–9). At polar latitudes, cold-stenothermy and increasing physical disturbance will shift and reduce the geographic ranges of high-latitude marine taxa, increasing their risk of extinction (10–12).

Globally accelerating temperature increases are already having profound effects on polar ecosystems. Those impacts extend beyond autecological responses to include top-down and bottom-up effects on marine food webs (13–17). The endemic faunas of the Antarctic continental shelf are now at risk of invasion by durophagous (skeleton-breaking) predators (18), a functional group that (based on the limited paleontological and genetic data available) may not have been ecologically significant there for as long as tens of millions of years (19–22).

"Reptant" (bottom-walking) decapod crustaceans, teleostean fishes, and neoselachian sharks and rays are key predators in shallow-subtidal communities worldwide but are at present physiologically excluded from nearshore environments in Antarctica (19). Reptant decapods, which include brachyuran crabs, anomuran crabs, and lobsters, typically cannot survive in waters colder than 1 °C, although adult stages of some of the more cold-tolerant taxa can survive down to 0.4 °C (23, 24). Their limited capacity to down-regulate naturally occurring magnesium ions in their hemolymph leads to paralysis and death at lower temperatures (25).

In the absence of durophagous predators, benthic faunas of the Antarctic shelf are lightly skeletonized and dominated by epifaunal suspension-feeders. The top predators are slow-moving invertebrates, such as seastars and nemertean worms. In some respects, therefore, Antarctic-shelf communities are reminiscent of low-predation communities living in contemporary deep-sea habitats, as well as communities from shallow, Paleozoic environments (26–30). Now, as sea temperatures rise, the reintroduction of durophagous predators could radically alter the composition and trophic structure of the shelf-benthos in Antarctica (19, 20, 31).

Lithodid crabs (Crustacea: Decapoda: Anomura) are common in the deep sea globally, as well as in shallow waters at subpolar latitudes (32). Also known as king crabs or stone crabs, lithodids

Significance

For tens of millions of years, cold conditions have excluded shell-crushing fish and crustaceans from the continental shelf surrounding Antarctica. Rapid warming is now allowing predatory crustaceans to return. Our study of the continental slope off the western Antarctic Peninsula showed that abundant, predatory king crabs comprise a reproductively viable population at 841- to 2,266-m depth. Depth profiles of temperature, salinity, habitat structure, food availability, and predators indicate that there are no barriers to prevent king crabs from moving upward onto the outer shelf at 400–550 m. A cold-water barrier above 200 m could be breached within the next few decades. Emergence of king crabs on the shelf could have catastrophic consequences for the unique seafloor communities of Antarctica.

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feed on a broad range of skeletonized invertebrates, but especially on echinoderms and mollusks (33–36). They are well known from deep-sea habitats of the Southern Ocean and are common in shallow, subantarctic waters (23, 37). Two species, *Paralomis birsteini* and *Neolithodes capensis*, were first observed on the continental slope adjacent to the western Antarctic Peninsula (WAP) in 2003, and these sightings were confirmed a few years later (38, 39). *P. birsteini* appears to be widespread in the Bellingshausen Sea and is the most commonly recorded lithodid species on the slope south of 60° S (18, 23, 37).

Phylogenetic evidence suggests multiple radiations of deep-sea lineages of lithodids into the Southern Ocean (32). How long they have been present on the Antarctic continental slope remains controversial (37), and there is virtually no information available on the status and viability of their populations. At some point, adult or larval *Neolithodes yaldwyni* must have moved over the shelf-break at ~500 m to establish a reproductively viable population at slope-depths >850 m in Palmer Deep, a trough carved into the shelf of the WAP by glacial movement (40). Lithodids are, however, currently excluded from nearshore, shallow-shelf environments along the WAP, because there the shallowest waters over the shelf are colder than the slope-waters (41–44). Although they are the most cold-tolerant of the reptant decapods, lithodids are still physiologically incapable of surviving below ~0.4 °C (18, 24, 32).

The bathymetric distribution of lithodids could change in the next few decades, however. Summertime sea-surface temperatures and temperatures of the Antarctic Shelf Bottom Waters off the WAP have risen by nearly 1.5 °C over the past 50 y, approximately double the globally averaged rate (45). Rising temperatures in shallow waters off the WAP will likely remove the thermal barrier to lithodids (and other reptant decapods) within the next several decades, facilitating their expansion into shallow, nearshore habitats (18). Judging from the strong, predatory role of invasive lithodids in Arctic food webs (33, 46), as well as the predatory impacts of the brachyuran snow crab *Chionoecetes opilio* in the Arctic (47), the effects of predation by lithodids could be severe in shallow-benthic communities in Antarctica (19, 40).

A recent critique (37) argued correctly that records of lithodids from the Antarctic slope and Palmer Deep do not by themselves constitute evidence that they could or will expand onto the shelf. Such a prediction could, however, be tested with time-series data on the population status and ecology of bathyal lithodids in Antarctica (37). Here, we take a significant first step in addressing that challenge. We describe a dense, reproductively viable population of *P. birsteini* living on the continental slope off the WAP. We show that there are no apparent physical or ecological barriers to impede the population from immediately expanding upward onto the deeper parts of the adjacent continental shelf, with potentially catastrophic impacts on the existing benthic fauna.

Results and Discussion

Population Structure of *P. birsteini*. In 2010, we conducted the first comprehensive survey of a population of lithodids on the Antarctic slope by towing the camera-vehicle SeaSled from the *RV Nathaniel B. Palmer* off Marguerite Bay, WAP (66°42′ S, 72°12′ W) (*Methods* and Fig. 1 *A* and *B*). SeaSled was towed at an average altitude of 3 m above the sediment–water interface. We completed eight photographic transects of the seafloor across the outer shelf, slope, and continental rise, covering a depth range of 385–2,285 m, a total distance of 72 km, and a total area of 183,653 m^2 (Fig. 1*A*, and Tables S1 and S2). The 38,018 pairs of overlapping, digital images we collected at altitudes of 0.5–6.0 m above the substrate were used to estimate population densities of *P. birsteini* across depths and assess reproductive viability. Tandem ecological assessments enabled us to evaluate the potential for lithodids to emerge on the shelf (Fig. 2).

We identified two taxa of lithodids using morphological features plainly visible in the images and in specimens retrieved in a trapping study off Marguerite Bay in 2015. Almost all of the king crabs were referable to *P. birsteini* (based on ref. 39), of which 468 individuals were found at depths of 841–2,266 m on the continental slope and continental rise (Fig. 1*C*). A species of *Neolithodes* referable to *N. yaldwyni* was also present but relatively rare, with five individuals observed on the continental slope at 989–1,209 m. The following discussion, therefore, pertains to *P. birsteini*.

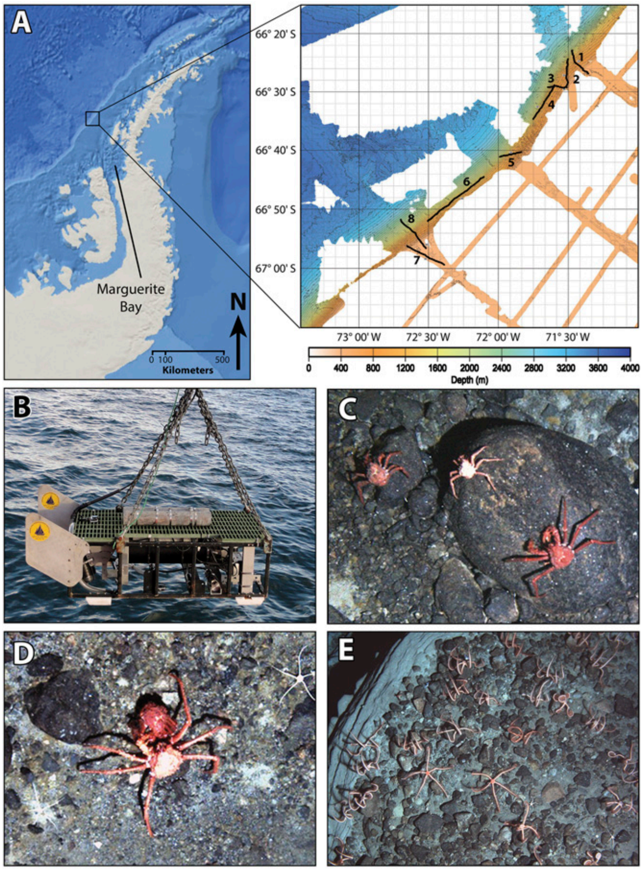

Fig. 1. Study site, SeaSled, and images from the seafloor. (*A*) Location of study site along the western Antarctic Peninsula. Expanded view shows known bathymetry of the study site, based primarily on multibeam data collected during the cruise. Numbered lines denote the eight transects (see Tables S1 and S2 for details). The depth gradient runs southeast to northwest; white areas represent unmapped portions of the seafloor. Map of Antarctic Peninsula on left produced in ArcGIS 10.2. (*B*) Towed camera-vehicle SeaSled being deployed. (*C*) Three *P. birsteini* at 1,356-m depth. (*D*) Pair of *P. birsteini* in precopulatory embrace at 841 m. Larger animal is the male. The female has recently molted, as inferred from her dark-red coloration. (*E*) Ophiuroids on the seafloor at 1,134 m.

Lithodids were absent from the continental shelf, which breaks at 400–550 m depth off Marguerite Bay. (The continental shelf in Antarctica is deeper than continental shelves elsewhere as a result of isostatic depression by the polar ice cap and glacial erosion of the shelf sediments.) Densities of *P. birsteini* were 0.3 individuals × 1,000 m^{-2} at 841- to 1,000-m depth and increased to a mean of 4.5 individuals × 1,000 m^{-2} over a depth range on the slope of 1,100–1,500 m (Fig. 2*B*). The maximum density of ~6 individuals × 1,000 m^{-2} at 1,200–1,300 m was lower than the density of lithodids in Palmer Deep (64°57′ S, 64°17′ W), but similar to the densities of other lithodid populations (40). A few individuals were found deeper than 1,600 m, but the limited area surveyed at those depths (Table S2) precluded an accurate estimate of population density.

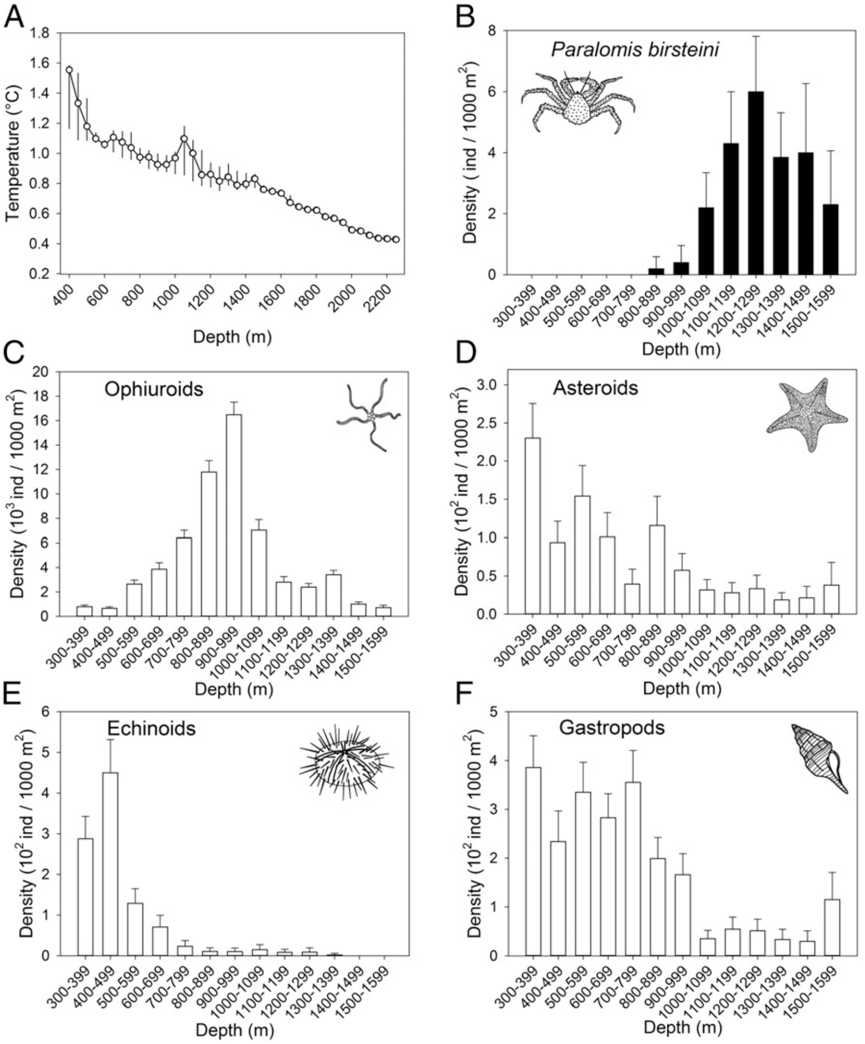

Fig. 2. Physical attributes and densities of invertebrates in the study area off Marguerite Bay, Antarctica. (*A*) Mean temperature in 50-m depth increments over the depth range sampled. Vertical bars represent ranges. (*B*) Density of *P. birsteini* with depth, over the depth range for which accurate estimates were possible. Error bars represent 95% confidence intervals. Means and confidence intervals were calculated assuming the data are Poisson-distributed within depth bins. (*C*–*F*) Densities of potential prey as a function of depth. Error bars represent 95% confidence intervals. Means and confidence intervals were calculated assuming the data for each prey-taxon are normally distributed within depth bins. Note the different depth scale in *A*, and the different scales of density in *B*–*F*.

Three pairs of *P. birsteini* were photographed in precopulatory embrace, which is the prelude to spermatophore transfer, at 841-, 1,095-, and 1,297-m depth (Fig. 1*D*). As in other anomuran crabs, the male lithodid is about a third larger and grasps the chelipeds of the female until she molts her exoskeleton, rendering her receptive to spermatophore transfer. The dark-red color of the female in Fig. 1*D* indicates a recent molt. Three discarded exoskeletons observed between 1,163 and 1,307 m also indicate that *P. birsteini* in this population were successfully molting. Significantly, four of the nine female *P. birsteini* recovered in the trapping study in 2015 were gravid, including one that was carrying eggs in the later stages of development (with fully developed eyes).

The mean carapace length (CL) of 146 *P. birsteini* that could be measured accurately from the images was 61.8 mm ± 0.15 SE (range 11.4–99.7 mm) (Fig. 3). Twenty-six individuals were <50-mm CL. Based on the age-structures of populations of similar-sized congeners in southern South America (48) and a single juvenile that was reported for this population in 2007 (39), these smaller individuals were classified as juveniles. The putative juveniles exhibited a broad bathymetric range of 1,126–2,266 m. Taken together with the large size of the population, our observations of precopulatory behavior, discarded molts, gravid females, and juveniles strongly suggest a reproductively viable population.

Habitat Characteristics of the Slope and Shelf.

Water temperature. Water temperatures were measured 1–6 m above the sediment–water interface using a CTD (conductivity–temperature–depth) instrument attached to SeaSled. Temperatures ranged from 0.43 to 1.6 °C at 385- to 2,285-m depth. The temperatures were highest on the continental shelf and negatively correlated with depth (Fig. 2*A*) (Pearson $r = -0.962$, $P < 0.001$). Along the same depth gradient, *P. birsteini* appeared on the slope at 841 m and increased rapidly in abundance, peaking at 1,200–1,300 m (Fig. 2*B*). *P. birsteini* were found at temperatures ranging from 0.43 °C at the deepest surveyed depth of 2,266 m on the continental rise to 1.16 °C at 1,039 m on the slope. The shallowest record was of two individuals at 841 m in an ambient temperature of 0.9 °C.

The thermal range of *P. birsteini*, ∼0.4–2.5 °C (24), as well as images collected off Anvers Island, 380 km to the northeast, strongly suggest that adults were actively feeding on the slope at

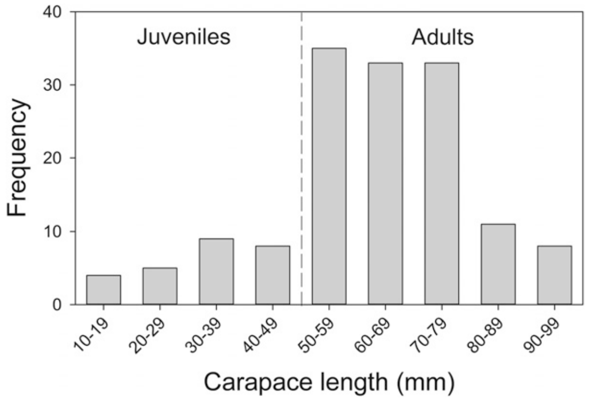

Fig. 3. Carapace lengths of *P. birsteini* imaged off Marguerite Bay, western Antarctic Peninsula ($n = 146$ crabs that could be measured from the images; 1,075- to 2,266-m depth). Vertical dashed line denotes the maximum carapace length of putative juveniles.

temperatures at least as low as 0.82 °C (49). Water temperatures on the upper slope (550–800 m) and lower (outer) shelf (400–550 m) were, therefore, within the known thermal tolerance of this species at the time of the survey, which was conducted in the austral summer. Temperatures in the austral fall and winter are generally greater than 1.0 °C at shelf depths below 200 m off Marguerite Bay, because of localized intrusions of the Circumpolar Deep Water (CDW) and a general, multidecadal trend of shallowing of the CDW in the Bellingshausen Sea (41, 45, 50, 51). A cold-water barrier to lithodids remains at depths above 200 m, where Antarctic surface water and winter water typically keep ambient temperatures below 0 °C year-round (41, 43). In contrast, cold Antarctic surface water can persist as deep as 500 m in parts of the Weddell and Ross Seas, suggesting that king crabs may be physiologically excluded from outer-shelf habitats in those locations (52).

Salinity. Salinity ranged narrowly from 34.9 to 36.0 psu over a depth range of 385–2,285 m. Salinity generally does not drop below 34.7 psu at depths of 300 m or more (41). The range of observed salinities on the shelf and slope falls within the tolerances of lithodid crabs, including *P. birsteini* (www.iobis.org/mapper/).

Sedimentary composition. We assessed the substrate preferences of *P. birsteini* by comparing the observed frequencies of sedimentary size-classes on the seafloor with the size-classes on which the lithodids were observed (Fig. 4*A*). The availabilities of four size-classes of sediment—fine-grained sediment, pebbles, cobbles, and boulders—were quantified in the depth range of maximum density of *P. birsteini*, 1100–1,500 m (*Methods*). The seafloor within that depth range was dominated by fine-grained sediment and pebbles (Fig. 4*B*). *P. birsteini* in 1,100–1,500 m were found most frequently on pebbles, but a greater number were associated with cobble and boulder substrates than expected in the null hypothesis (*G*-test: $G = 215.70$, $\mathrm{df} = 3$, $P < 0.001$) (Fig. 4*A*). There were no significant differences in the proportions of the four sedimentary categories between 1,100–1,500 m and 400–600 m (Fig. 4*B*) (Mantel test: $r = –0.160$, $P = 0.22$). Combining the distribution of *P. birsteini* on the sedimentary categories at 1,100- to 1,500-m depth with the relative abundances of those categories at 400–600 m, we calculate that, absent other constraints, *P. birsteini* has the potential to reach densities of 4.5 individuals × 1,000 m^{-2} within that depth range.

Hydrostatic pressure. We observed *P. birsteini* at a minimum depth of 841 m on the slope off Marguerite Bay. The shelf-break off Marguerite Bay extends at least to 550 m, which is well within the known depth range of the species. *P. birsteini* has been collected as shallow as 341 m on a seamount outside the Ross Sea (53), and other lithodids have been collected at 200 m or shallower off islands and seamounts surrounding Antarctica (23, 37, 54). Deep-water lithodids can be maintained for months in the laboratory at atmospheric pressure without any noticeable adverse effects (55, 56). Hydrostatic pressure should not, therefore, present a barrier to *P. birsteini* expanding onto the outer shelf off Marguerite Bay.

Many benthic invertebrates in Antarctica are eurybathic because the water column is uniformly cold. Ecological and evolutionary emergence of deep-water taxa in shallow water and submergence of shallow-water taxa in deep water are historical phenomena more common in Antarctica than at lower latitudes. These bathymetric shifts have been driven by glacial dynamics in the Neogene and have not been impeded by the effects of temperature or hydrostatic pressure (27, 57). Furthermore, movement of lithodids onto the outer Antarctic shelf—and shoreward as sea temperatures rise—would repeat their expansion onto the Patagonian shelf during deglaciation 10,000 y ago (20). Clearly the emergence of lithodids is physiologically and ecologically feasible. The acceleration of that emergence by anthropogenic climate change and the capacity of the lithodids for durophagous predation are features that would make their appearance on the Antarctic shelf ecologically novel and potentially transformative.

Distribution of prey resources. The availability of food resources across depths was evaluated by estimating the population densities of the known prey of lithodids visible in images taken 0.5–3.0 m above the substrate: ophiuroids, asteroids, echinoids, and gastropods. Potential prey that were not visible in the images, such as infaunal bivalves, could not be evaluated. The density of ophiuroids formed a unimodal distribution that peaked at 900–1,000 m (Figs. 1*E* and 2*C*). The overlapping tails of the depth distributions of ophiuroids and *P. birsteini* suggested an inverse relationship (Fig. 2 *B* and *C*). Asteroids, echinoids, and gastropods were more abundant at all shelf depths and generally more abundant on the upper slope than they were at 1,100–1,500 m (Fig. 2 *D*–*F*), suggesting that predation by *P. birsteini* may limit the distributions of these taxa. A similar disjunction in depth distribution of *N. yaldwyni* and echinoderms was observed in Palmer Deep (40), and *C. opilio* and ophiuroids were distributed in a complementary pattern in the Chukchi Sea (47). Considering the generality of diet in lithodids and their predilection for echinoderms and mollusks, there is no reason to expect that the population of *P. birsteini* would be food-limited were it to expand to the outer shelf.

Predation pressure. Potential predators of benthic decapods include fishes, marine mammals, cephalopods, and other crustaceans in temperate, tropical, and Arctic marine ecosystems. The demersal fish fauna of Antarctica is comprised almost exclusively of three taxa of teleosts: the suborder Notothenioidei, distributed primarily in shelf environments; the family Zoarcidae on the slope; and the family Liparidae on the deep slope and continental rise. Fishes

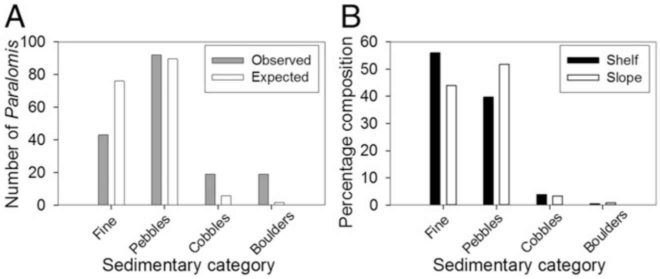

Fig. 4. Sedimentary composition and preferences of the lithodid crab *P. birsteini* along the western Antarctic Peninsula. (*A*) Observed and expected frequencies of *P. birsteini* on different sedimentary categories on the slope (1,100–1,500 m; $n = 173$). Expected values were calculated assuming the crabs showed no preferences for sedimentary categories. (*B*) Sedimentary composition on the continental shelf (400–600 m) and slope (1,100–1,500 m). Frequency data were converted to percentages for ease of comparison ($n = 3,000$ for the shelf; $n = 6,000$ for the slope).

were rarely observed along the transects (58). Based on biomechanical analysis of the demersal teleosts, limited durophagous feeding is possible in notothenioids and zoarcids, but not in liparids (59). Some teleostean taxa might be capable of preying on the demersal larvae or juveniles of *P. birsteini*, but the few data available on their diets, distributions, and feeding biomechanics suggest that these fishes are not durophagous (59).

Nevertheless, published observations of predation on lithodids raise the possibility that their emergence onto the shelf may not be risk-free. The Antarctic toothfish *Dissostichus mawsoni*, a nektonic notothenioid, occasionally preys on lithodids at subantarctic latitudes, especially species such as *P. birsteini* that lack spiny exoskeletons; *P. birsteini* have been identified in the stomach contents of toothfish (54). Although *D. mawsoni* are present in the depth range in which we observed *P. birsteini*, they are extremely rare at all depths off Marguerite Bay (58) and are unlikely to pose a threat. Similarly, although skates (Rajidae) and larger octopods potentially could feed on *P. birsteini* in outer-shelf and slope habitats, they appeared only rarely in our images. Neither octopods nor skates play a significant role in Antarctic food webs (19).

Seals, which feed primarily on fish, cephalopods, and krill, could also prey on lithodids. Based on the diets of Antarctic seal species, the most likely candidates are Weddell seals, *Leptonychotes weddellii*, and southern elephant seals, *Mirounga leonina*. Weddell seals are known to feed on small crustaceans and can dive to at least 726 m, although their depth range is generally on the order of 100–200 m (60, 61). Male elephant seals, which dive to an average depth of 500 m, occasionally feed on benthic crustaceans (62). Neither species of seal is likely to pose a significant threat to *P. birsteini* on the outer shelf.

We estimated predation pressure on the population of *P. birsteini* by assessing the extent of sublethal damage, in the form of missing or regenerating chelipeds and walking legs. Injuries to limbs were rare: of 347 *P. birsteini* that could be assessed from the images, 31 individuals, or 8.9%, displayed one or more damaged limbs. Of the 2,776 limbs of these animals that were visible in the images, 34, or 1.2%, were damaged. This latter incidence of damage was low compared with temperate decapods [e.g., 22.8% in the blue crab *Callinectes sapidus* (63)], despite lower regeneration rates in colder, Antarctic waters. The incidence of damage in *P. birsteini* was also low compared with the lithodid *Paralithodes camtschaticus* in the Arctic [16.1% incidence (63)]. Chelipeds are often damaged in mating and other intraspecific interactions, so the low percentages for *P. birsteini* probably overestimate the frequency of interspecific, sublethal predation. Regardless, the low level of sublethal damage and the paucity of potential predators strongly suggest that both sublethal and lethal predation events are rare.

Conclusion

We found a reproductively viable population of the lithodid crab *P. birsteini* resident on the continental slope off Marguerite Bay, western Antarctic Peninsula. Although the history of this population is unknown, its contemporary ecology supports the idea that bathyal lithodids could expand upward within a few decades. Depth profiles of water temperature, salinity, sedimentary composition, and the availability of prey, as well as the general absence of predators, indicate conditions favorable to upward expansion of *P. birsteini* in this location, at least as shallow as the lower depths of the continental shelf. *P. birsteini* would likely have a pervasive impact on the resident shelf-benthos, as lithodids do in other low-temperature environments around the world. Long-term ecological monitoring off Marguerite Bay and additional locations around Antarctica will be the only way to test rigorously the hypothesis of an imminent or ongoing expansion of lithodids into shelf habitats (37). Our study provides the initial data for such a long-term study.

Declining temperatures in the Southern Ocean after the Eocene drove benthic communities on the Antarctic shelf from a typically Cenozoic structure and function to the retrograde, quasi-Paleozoic character they exhibit today. Anthropogenic climate change is now rapidly rewarming the Southern Ocean, potentially reversing this trend. At present rates of warming, lithodids should be able to survive in inner-shelf and coastal environments (above 200 m) within several decades. Emergence of predatory lithodids on the continental shelf could be a critical step toward remodernizing benthic communities in Antarctica and functionally homogenizing them with benthic-shelf communities at lower latitudes. Such changes would fundamentally alter the Antarctic benthos and diminish the global diversity of marine ecosystems.

Methods

A photographic survey of the continental slope and shelf off Marguerite Bay was conducted from the *RV Nathaniel B. Palmer* in early December 2010 during National Science Foundation cruise NBP10-05. Eight transects, averaging 9 km in length, were imaged within a 100 × 100-km study site (Fig. 1 and Table S1). Transects covered the outer continental shelf, slope, and rise from 385- to 2,285-m depth. Images of the seafloor were obtained using the towed camera-vehicle SeaSled, which is owned and operated by the Woods Hole Oceanographic Institution, Woods Hole, MA (58, 64). SeaSled was equipped with two cameras (each 1.4-megapixel, or 1,360 × 1,024 pixels), two strobes (150 w-s), an acoustic-Doppler current profiler (1,200 kHz; Teledyne RD Instruments), a depth sensor (Paroscientific), and a CTD (Seabird SBE-49 Fast CAT 16-Hz). Two overlapping, strobe-lit images were collected every 3 s at an average altitude of 3 m above the substrate. The altitudinal range of usable images was 0.5–6.0 m above the substrate.

Density and Size Estimates. Densities were estimated for *P. birsteini* and four taxa of benthic prey: ophiuroids, asteroids, echinoids, and gastropods. Image clarity was reduced with increasing altitude from the seafloor, and all images collected at an altitude above 6 m were discarded. The remaining images, which comprised 38,018 image pairs, were pooled, divided into 100-m depth bins, and used to estimate the density of *P. birsteini*.

A density estimate was calculated for *P. birsteini* within each depth bin in each transect. For each depth bin, the number of crabs in each transect was divided by the total area covered by the images from that transect within that depth bin, corrected for the overlap of the image pairs and between adjacent image pairs along the transect. The planar area of each image was determined trigonometrically from its dimensions and the altitude of the camera. The mean density of crabs per 1,000 m^2 and the 95% confidence intervals within each depth bin were calculated assuming a Poisson distribution, because the crabs were rare in the images.

The potential prey were smaller and more abundant than *P. birsteini*, and accurate density estimates could only be obtained from images taken at a maximum altitude of 3 m. Densities were estimated using 250 randomly selected images from each depth bin, with the exception of 1,400–1,500 m and 1,500–1,600 m. Only 132 and 71 images, respectively, were available at altitudes of 3 m or less in those depth bins. The 95% confidence intervals were calculated assuming the prey taxa were normally distributed within each depth bin.

Where possible, the carapace lengths of the lithodids were measured based on the dimensions of the area captured in the image, using the software package Coral Point Count with Excel extensions (65). Measurements were only recorded for individuals observed on a horizontal plane and for which the entire carapace could be seen, at a maximum altitude of 3 m (i.e., the carapace and appendages had to appear symmetrical in the image).

Assessment of Benthic Habitat. Temperature and salinity data recorded 1–6 m above the seafloor were pooled from all transects and averaged at each 50-m depth mark, from 400 to 2,250 m. For each 50-m depth mark, z, the temperature and salinity data from $z \pm 10$ m were used.

The composition of the substrate was determined for the shelf (400–600 m) and slope (1,100–1,500 m) using 100 randomly selected images from a maximum altitude of 3 m from each 100-m depth bin. Fifteen points were randomly placed on each image within a standardized 1-m^2 plot using Coral Point Count with Excel extensions. The grain of sediment beneath each point was measured and classified into one of four size-categories: fine-grained sediment (grain-size < 4 mm), pebble (4 to <64 mm), cobble (64 to <256 mm), or boulder (≥256 mm). In a pilot study using different numbers of random points, we determined that 15 points per image were sufficient to make accurate assessments of coverage of the different size-classes of sediments. Each *P. birsteini* photographed from a maximum altitude of 3 m was also analyzed to determine the size-class of sediment beneath it. A *G*-test was used to compare the observed frequency of *P. birsteini* on each size-class of sediment to the frequency expected under the assumption that they had no grain-size preference. The proportions of sedimentary size-classes between the shelf and slope were compared using a Mantel test.

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Supporting Information

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Table S1. Details of the eight transects imaged within the 100 × 100-km study area off Marguerite Bay, western Antarctic Peninsula

Transect	Minimum depth (m)	Maximum depth (m)	Length of transect (m)	Number of image pairs	Area covered (m^2)	Start latitude/ longitude	End latitude/ longitude
1	497	1,390	6,950	4,619	21,817	66°26′37′′ S 71°21′52′′ W	66°22′53′′ S 71°28′28′ W
2	562	1,535	7,326	4,189	19,436	66°24′35′′ S 71°30′09′′ W	66°29′42′′ S 71°30′38′′ W
3	586	1,310	3,987	2,370	13,468	66°29′39′′ S 71°31′09′′ W	66°29′57′′ S 71°38′40′′ W
4	1,037	1,316	7,884	3,610	18,516	66°29′24′′ S 71°36′39′′ W	66°34′35′′ S 71°44′51′′ W
5	626	1,527	6,090	3,262	17,154	66°40′32′′ S 71°48′23′′ W	66°41′36′′ S 71°59′57′′ W
6	1,109	1,398	18,664	10,438	45,535	66°44′29′′ S 72°06′20′′ W	66°52′00′′ S 72°30′46′′ W
7	385	642	11,114	5,403	25,656	66°56′12′′ S 72°39′26′′ W	66°59′25′′ S 72°23′14′′ W
8	409	2,285	9,566	4,127	22,071	66°52′17′′ S 72°40′49′′ W	66°56′30′′ S 72°31′11′′ W
TOTAL			71,581	38,018	183,653		

Table S2. Area per depth range for the eight transects imaged within the 100 × 100-km study area off Marguerite Bay, western Antarctic Peninsula

	Area (m^2) per depth range								
Depth (m)	Dive 1	Dive 2	Dive 3	Dive 4	Dive 5	Dive 6	Dive 7	Dive 8	Total area (m^2)
300–399	—	—	—	—	—	—	3,884	—	3,884
400–499	286	—	—	—	—	—	20,564	6,218	27,068
500–599	5,387	4,086	301	—	—	—	790	869	11,433
600–699	2,376	2,286	2,865	—	2,036	—	418	674	10,655
700–799	2,218	2,946	2,291	—	2,407	—	—	1,299	11,161
800–899	2,771	3,432	1,567	—	2,738	—	—	1,159	11,667
900–999	2,222	1,064	1,915	—	1,523	—	—	859	7,583
1,000–1,099	2,129	884	1,678	7,732	2,181	—	—	687	15,291
1,100–1,199	1,737	—	1,922	4,850	1,681	8,730	—	552	19,472
1,200–1,299	1,871	843	842	5,578	1,423	9,769	—	608	20,934
1,300–1,399	820	1,907	87	356	1,314	27,036	—	987	32,507
1,400–1,499	—	1,246	—	—	1,438	—	—	807	3,491
1,500–1,599	—	742	—	—	413	—	—	768	1,923
1,600–1,699	—	—	—	—	—	—	—	681	681
1,700–1,799	—	—	—	—	—	—	—	843	843
1,800–1,899	—	—	—	—	—	—	—	765	765
1,900–1,999	—	—	—	—	—	—	—	971	971
2,000–2,099	—	—	—	—	—	—	—	1,314	1,314
2,100–2,199	—	—	—	—	—	—	—	1,009	1,009
2,200–2,299	—	—	—	—	—	—	—	1,001	1,001
Total area (m^2)	21,817	19,436	13,468	18,516	17,154	45,535	25,656	22,071	

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