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From deep to shallow seas: Antarctic king crab on the move

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The fauna of decapod crustaceans in the Southern Ocean has historically been considered impoverished, with only about a dozen species of decapod shrimp overall, of which only three species are common and abundant on the Antarctic continental shelf. Crabs and lobsters were assumed to be absent or very rare in the Southern Ocean, mainly ascribed to the physiological constraint of cold polar waters. Polar temperatures have been hypothesised to reduce decapod activity, especially in combination with high magnesium levels in the haemolymph ($[Mg^{2+}]_{HL}$), as $[Mg^{2+}]$ has a relaxant effect. Mg^{2+} is abundant in seawater and in combination with polar temperatures causes relaxant effect in Crustacea (Frederich et al., 2001). Since most crabs are capable of regulating $[Mg^{2+}]_{HL}$ only slightly below the $[Mg^{2+}]$ of seawater, their ability to maintain activity should be hampered (Frederich et al., 2001, Aronson et al. 2015a). In contrast, caridean shrimp regulate $[Mg^{2+}]_{HL}$ to very low levels. The combined effect of low temperatures and high $[Mg^{2+}]_{HL}$ might explain the limits of cold tolerance in decapods and has been put forward as the principal reason for the absence of crabs and lobsters from the high-polar regions (Frederich et al., 2001, Aronson et al., 2015a). These large, benthic, shell-crushing decapods, along with shell-crushing teleosts and elasmobranchs, are important in structuring benthic communities at lower latitudes.

In 2004, a review of rare and scattered literature records of crab from the Southern Ocean revealed that some crabs might be more common than previously believed (Thatje and Arntz, 2004, Thatje et al., 2005). Indeed, the anomuran crab family Lithodidae, also known as stone or king crab, revealed about a dozen species recorded from waters off islands, seamounts, and the general Antarctic deep sea. The study also revealed that the high-Antarctic continental shelves, where temperatures have historically been -1.9 °C, are completely free of these seafloor predators. This is important, as the continental shelves of the high Antarctic are dominated by unique communities of sessile and slow-moving epifaunal invertebrates that have evolved in the absence of shell-crushing predators for millions of years, at least since the last cooling step of Antarctica until about 16 Ma ago (Thatje et al., 2005). Now, in light of climatic warming, it has been hypothesised that predatory king crabs (Lithodidae) living in the upper bathyal zone could emerge onto the continental shelf and into nearshore habitats, and that their predatory activity would put the unique benthos of the shelf at risk (Thatje et al., 2005, Aronson et al., 2015b).

Increased sampling effort in the deep waters off the Western Antarctic Peninsula (WAP) since the millennium revealed that lithodid crabs are more common and widespread than previously believed, and two species of lithodids have now been recorded in abundance at continental-slope to abyssal depths (Thatje and Arntz, 2004, Smith et al., 2012, Aronson et al., 2015b). *Paralomis birsteini* (Fig. 1a) is the most abundant and widely distributed species, showing reproductively viable populations on the continental slope and rise at 721–2,266 m water depth. In 2005, Garcia Raso et al. (2005) described the species for the deeper continental slope off the WAP, followed by a slightly shallower record in 2008 (Thatje et al., 2008). Even shallower records close to the continental shelf-break (minimum 721 m) were revealed by three US seagoing expeditions, which studied two abundant and established populations off the WAP (Aronson et al., 2015b). A species of *Neolithodes* assigned to *N. yaldwyni* was also found off the WAP but was relatively rare, with five individuals observed on the continental slope at 989–1,209 m (Aronson et al., 2015b) and an established population detected at continental-slope depths (>850 m) of the Palmer Deep (Smith et al., 2012).

Here, we provide insight into the biology of *P. birsteini* based on 96,786 usable images of the deep ocean floor taken by towing a camera system 0.5–4 meters above the ocean floor (Fig. 1c-e), during three ship-based US expeditions targeting the continental shelf and slope off the WAP, off Anvers Island (66°30 S) and Marguerite Bay (66°42 S) (Aronson et al., 2015b, Smith et al., 2017a, b). These images revealed 1,360 *P. birsteini*, often depicting distinct stages of their life cycle. Alongside the photographic transects, baited traps were deployed during two of the three expeditions, giving further insights in the crabs' biology.

The occurrence of crabs was generally associated with coarse sediments of glacial origin characterised by pebbles and glacial drop stones (Fig. 1d, e), substrata preferred by the genus. Surprisingly, eight juveniles (< 1cm carapace length) were found sitting on top of large sea stars, which poses the question of whether this host serves as a substratum for postlarval settlement, as well as a potential food source or provider of food to crabs in commensalistic behaviour. The recruitment and survival of deep-sea lithodid crab larvae remains completely unexplored, which makes the starfish association of juvenile crabs a significant observation, as echinoderms constitute a major food source of adult lithodid crabs (Smith et al., 2017b), and biological substratum for larval settlement is generally assumed to be scarce in the deep sea. This observation is supported by a record of juvenile lithodid crab associated with deep-sea starfish in the North Atlantic at about 1587 m water depth (see Fig. 18 in: Mah, 2020).

Adult *P. birsteini* moults were observed in several images, as well as adult specimens in moult. The two populations (Anvers Island and Marguerite Bay) were reproductively active, as shown by precopulatory embrace (Fig. 1c), in which the always-larger male carries and protects the female throughout the moult or postmoult stages. Alongside towing a camera system for deep-sea imaging, baited traps had been deployed. Four out of nine females caught in the baited traps were in the ovigerous stage, carrying large eggs at various stages of development (Smith et al., 2017a, Fig. 1b), possibly indicating asynchrony in reproductive activity. Fecundity was low, with 1891–2308 eggs per specimen. Given that a congener from the Southern Ocean, *P. spinosissima* from South Georgia, carries its eggs for about two years before hatching larvae, and that *in situ* temperatures are similar between the two locations, a similarly slow embryogenesis should be assumed in *P. birsteini.* The eggs are exceptionally large (~2.0 mm in diameter) and contain high amounts of lipids, indicating high per-offspring investment by mothers (Fig. 1b). Prezoea stage hatched aboard a research vessel upon recovery of females revealed that the larvae rely on high levels of energy reserves of maternal origin. Larval development appears, therefore, to be fully lecithotrophic as is generally the case for deep-sea lithodids (Hall and Thatje, 2009, Thatje and Hall, 2016). A hypometabolic way of life of food-independent larvae at polar temperatures predicts very slow larval and early juvenile development (Thatje et al., 2005). *Paralomis birsteini* thrives at the thermal limits known for the family and, therefore, life-history processes are expected to be slow (Thatje et al., 2005, Hall and Thatje, 2011); this should imply slow growth and high age at maturity, as well as high expected maximum age. The overall life-history data indicate that populations of *P. birsteini* off the WAP are viable and reproductively active; however, most of the life cycle of the species remains to be studied in more detail.

A gut-content study of thirty specimens of *P. birsteini* recovered using the baited traps showed that the species is omnivorous (Smith et al., 2017b). The most-prevalent food items were ophiurods, followed by mollusks (gastropods and bivalves), and echinoids. Asteroids, holothurians, polychaetes, bryozoans, and poriferans were also identified in the gut contents. A study of macrobenthic abundance in areas with and without abundant crabs showed that *P. birsteini* is capable of structuring the benthic community by significantly reducing its prey items (Smith et al., 2017b). The species is opportunistic and was also found to scavenge a whale-fall off Anvers Island (Smith et al., 2014).

But are we presently witnessing a population expansion in *P. birsteini*? It remains a subject of scientific (and semantic) discussion whether or not the species is potentially invasive of the Antarctic shelf-break, threatening the pristine seafloor communities of the shelf. Indeed, evidence suggests that the thermal barrier to range expansions into outer-shelf waters off the WAP has already been lifted by climatic warming (Aronson et al., 2015) above about 0.4-0.5 °C, the family-specific thermal threshold to activity (Thatje et al., 2005, Hall and Thatje, 2011).

Both continental slope populations studied in more detail, from waters off Anvers Island and Marguerite Bay, show that the seafloor communities suffer from predation at distinct levels, with Marguerite Bay showing a higher predatory pressure by crabs than Anvers Island (Smith et al., 2017b). Given the high percentage of adults in the Marguerite Bay population this may indicate that both predator populations are at distinct levels of development, which is also indicated by higher densities of crabs off Marguerite Bay (Smith et al., 2017b). Such population-specific differences could be indicative of different levels in the expansion of mature communities. Lithodid crabs are known to move and migrate in large collections, a behaviour used by fisheries at lower latitudes to target them. Few juveniles have been observed, possibly due to a lack of image-resolution, or the juveniles might have been hiding under rocks.

Importantly, population-genetic work has shown that the population of *P. birsteini* off Marguerite Bay may have expanded in the geological past, at least twice within the last 132,000 years (Hellberg et al., 2019). Oscillations in past climate were the most likely drivers of such population expansions, with warming seas opening up habitat to crabs. Further study of the movements of the crabs on different time-scales, as well as their molecular past, will reveal whether we are currently witnessing an third warming-mediated invasion by these predatory crabs of continental-shelf waters along the WAP. Expansion of lithodids into continental-shelf habitats could fundamentally alter benthic-community structure and homogenize it with community structure in shallow seas elsewhere, where the seafloor communities are generally structured from the top down by shell-breaking predators (Aronson et al., 2015b).

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Literature Cited

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., K. E. Smith, S. C. Vos, J. B. McClintock, M. O. Amsler, P.-O. Moksnes, D. S. Ellis, J. Kaeli, H. Singh, J. W. Bailey, J. C. Schiferl, R. van Woesik, M. A. Martin, B. V. Steffel, M. E. Deal, S. M. Lazarus, J. N. Havenhand, R. Swalethorp, S. Kjellerup and S. Thatje. 2015b. No barrier to emergence of bathyal king crabs on the Antarctic shelf. Proceedings of the National Academy of Sciences of the USA 122:12997–13002.

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.

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.

Hellberg, M. E., R. B. Aronson, K. E. Smith, M. I. Duhon, S. T. Ahyong, G. A. Lovrich, S. Thatje and J. B. McClintock. 2019. Population expansion of an Antarctic king crab? Frontiers of Biogeography 11.3: e4316

Mah, C. L. 2020. New species, occurrence records and observations of predation by deep-sea Asteroidea (Echinodermata) from the North Atlantic by NOAA ship Okeanos Explorer. Zootaxa 4766:201–260.

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, Series B 279:1017–1026.

Smith, K. E., S. Thatje, H. Singh, M. O. Amsler, S. C. Vos, J. B. McClintock, A. Brown, D. Ellis, C. J. Brothers, J. Anderson and R. B. Aronson. 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.

Smith, K. E., R. B. Aronson, S. Thatje, G. A. Lovrich, M. O. Amsler, B. V. Steffel and J. B. McClintock. 2017a. Biology of the king crab *Paralomis birsteini* on the continental slope off the western Antarctic Peninsula. Polar Biology 40:2313–2322.

Smith, K. E., R. B. Aronson, B. V. Steffel, M. O. Amsler, S. Thatje, H. Singh, J. Anderson, C. J. Brothers, A. Brown, D. S. Ellis, J. N. Havenhand, W. R. James, P. O. Moksnes, A. W.

Randolph, T. Sayre-McCord and J. B. McClintock. 2017b. Climate change and the threat of novel marine predators in Antarctica. Ecosphere 8(11): e02017.

Thatje, S. and W. E. Arntz. 2004. Antarctic reptant decapods: more than a myth? Polar Biology, 27:195–201.

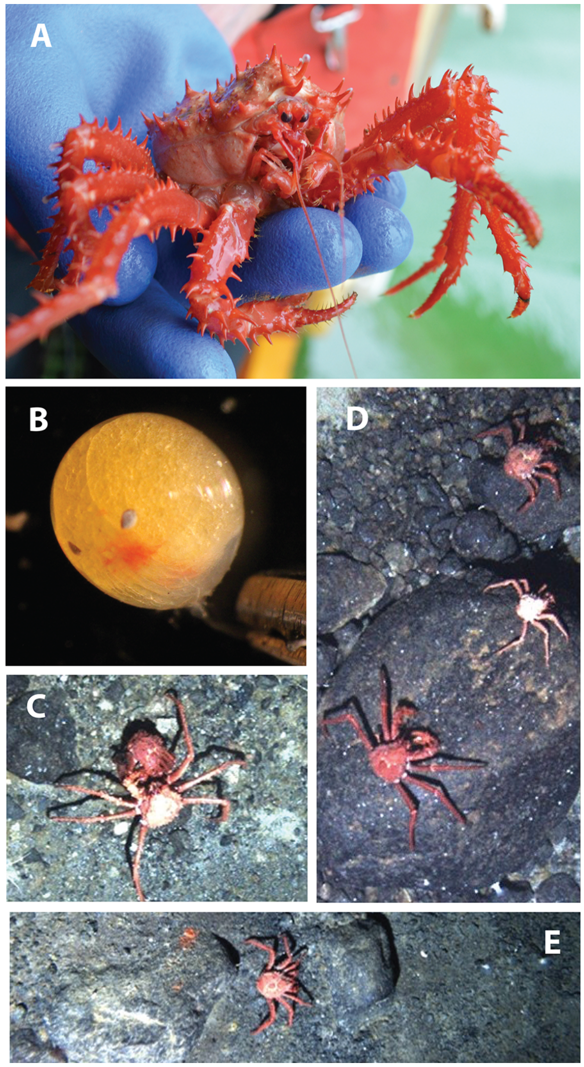
Thatje, S., K. Anger, J. A. Calcagno, G. A. Lovrich, H. O. Pörtner and W. E. Arntz. 2005 Challenging the cold: crabs reconquer the Antarctic. Ecology 86:619–625.

Thatje, S., S. Hall, C. Hauton, C. Held and P Tyler. 2008. Encounter of lithodid crab *Paralomis birsteini* on the continental slope of Antarctica, sampled by ROV. Polar Biology 31:1143–1148.

Thatje, S. and S. Hall. 2016. The effect of temperature on the evolution of per offspring investment in a globally distributed family of marine invertebrates (Crustacea: Decapoda: Lithodidae). Marine Biology 163:48.

Figure Legend

Fig. 1. The lithodid crab *Paralomis birstini* in Antarctic waters off the Western Antarctic Peninsula (WAP). (A) Anterior view of specimen of *P. birsteini*; (B) Yolk-rich egg (2.0 mm in diameter) with embryo and dark eye placodes clearly visible; (C) Pair of *P. birsteini* in precopulatory embrace at 841m, with recently moulted female (upper specimen); (D, E) specimens of *P. birsteini* among boulders on continental slope off Marguerite Bay, WAP (the two red laser dots in (E) are 10 cm apart).



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