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Population expansion of an Antarctic king crab?

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Abstract. Benthic assemblages of the Antarctic continental shelf are dominated by sessile and slow-moving, epifaunal invertebrates. This community structure persists because shell-crushing (durophagous) predators are absent or ecologically insignificant in shelf habitats. Durophagous teleosts, elasmobranchs, and crustaceans have been excluded by cold waters over the Antarctic shelf for millions of years. Now, as shallow waters warm rapidly, predatory king crabs (Lithodidae) living in the upper bathyal zone could emerge onto the shelf and into nearshore habitats. To assess the potential for a bathymetric expansion, we genetically inferred the historical demography of a population of the most abundant durophagous predator found in deep water off the western Antarctic Peninsula: the lithodid *Paralomis birsteini* Macpherson. Analysis of mitochondrial DNA sequences from crabs sampled at 1200–1400 m depth on the slope off Marguerite Bay suggests this population has expanded twice over the past 132,000 years. Those expansions were possibly coincident with episodes of climatic warming in Antarctica and elsewhere, raising the possibility of a third expansion in response to anthropogenic climate change.

Keywords: Antarctica; marine; invasive predator; historical demography; deep sea; ocean warming; polar

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Introduction

Climate change is altering the composition and dynamics of marine communities at all latitudes (Doney et al. 2012, Poloczanska et al. 2013). Rapidly rising temperatures over the continental shelf off the western Antarctic Peninsula (Schmidtko et al. 2014) may be facilitating the reappearance of shell-crushing or durophagous predators, which have been absent from or ecologically insignificant in the cold environment of the Antarctic shelf for millions of years (Aronson et al. 2007, 2015). Thermal exclusion of durophagous teleosts, elasmobranchs, and decapod crustaceans, which exert significant top-down control on benthic communities elsewhere, has fostered a unique fauna of ophiuroids, nemertean worms, asteroids, pycnogonids, brachiopods, molluscs, and other sessile and slow-moving epifaunal invertebrates, driving the shelf-benthos in Antarctica toward a retrograde community structure with Paleozoic affinities (Aronson et al.

2007, Watson et al. 2017). By allowing durophagous predators to return, anthropogenic climate change could shift those dynamics, compromising the unique community structure of the Antarctic bottom-fauna.

King crabs (Lithodidae), which inhabit the slightly warmer waters of the upper continental slope, could be the vanguard of an invasion of shell-crushing predators in Antarctic shelf habitats (Aronson et al. 2015, 2017). Whether they can be considered invasive on the slope or whether they have been present there for millions of years remains an open question (Griffiths et al. 2013). The question cannot be resolved by the fossil record, because the Neogene record of decapod crustaceans is poor in Antarctica, having been largely erased by repeated ice-scour. Fossils, however, are not the sole remnants of information left by past populations.

Populations of different sizes should contain different levels of genetic variation, with larger populations expected to harbor more variation than smaller ones. Past changes in population size can thus be detected by inspection of the distribution of sequence divergences between alleles in present-day populations. Demographic expansions stamp a particular genetic impression on a population: an excess of closely related alleles that such growth creates relative to populations that remain stable.

Here, we test for genetic signals of past demographic expansion in the Antarctic king crab *Paralomis birsteini*. *Paralomis birsteini* is the most common durophagous predator in the bathyal zone off the western Antarctic Peninsula (WAP). The species was initially thought to be restricted to deep water, but surveys off the WAP over the past 20 years have recorded them within 200–300 bathymetric meters of the shelf-break at ~500 m (Aronson et al. 2015). Genetic analysis of samples gathered from one such population suggest it has expanded twice in the last 6000 generations.

Methods

Sampling and collection of genetic data

Crabs were trapped at 1200–1400 m depth in a 100 × 100 km area off Marguerite Bay centered at 66°42'S, 72°12'W during an oceanographic cruise in 2015 (Smith et al. 2017). Leg muscles were preserved in >70% ethanol and stored at or below -20°C. DNA was extracted from samples of 50 individuals using the Qiagen DNeasy Blood & Tissue Kit. We amplified a portion of the mitochondrial *cytochrome oxidase subunit I (COI)* gene (Folmer et al. 1994), using standard PCR protocols with a 50°C annealing temperature. Amplicons were sequenced in both directions on an ABI 3130XL at the Louisiana State University Genomics Facility using the amplification primers. Sequences were aligned using 4Peaks (Griekspoor and Groothuis 2017)¹. No indels were evident.

Genetic analyses

We used three summary statistics to test for departures from a constant population size: Tajima's D (Tajima 1989), F_s (Fu 1997), and R_2 (Ramos-Onsins and Rozas 2002). Populations that have expanded recently should produce negative values for the first two and positive for the last, although selective sweeps can produce the same result. Of the three, coalescent simulations show that R_2 is the most powerful for small sample sizes (Ramos-Onsins and Rozas 2002). All three were calculated using DnaSP 6 (Rozas et al. 2017).

As an initial test for whether the data show any evidence of a past population expansion, we compared models for population size with and without a parameter for past population growth using a Bayesian coalescent analysis (LAMARC) (Kuhner 2006). Relationships among sequences were further analyzed to infer when changes in population size likely occurred. The intervals between when the histories of different alleles coalesce

(i.e., join together in common ancestral sequences) can be used to infer changes in population size. Historical population sizes were reconstructed using the GMRF skyride plot (Minen et al. 2008) implemented in BEAST 1.10. We performed two runs of 10 million generations sampling every 1000. Output files were checked (all Effective Sample Sizes were greater than 250) and visualized in Tracer 1.6 (Rambaut et al. 2018).

Population sizes and dates provided by GMRF skyride plots were scaled by generation time and nucleotide substitution rate. The known generation times of lithodid species are generally on the order of 5–6 years (Grant and Cheng 2012, Hall and Thatje 2018). The generation time of *P. granulosa*, a congener of similar size from Argentina, is 12 years (Lovrich and Vinuesa 1999). The larval-development time of *P. spinosissima*, which—like *P. birsteini*—lives at ~1°C, is twice that of *P. granulosa*, which lives at ~6°C, even when *P. spinosissima* is raised at 5°C (Anger et al. 2003, Thatje and Mestre 2010). Based on this doubling of larval-development time of *P. spinosissima* compared with *P. granulosa*, we estimated the generation time of *P. birsteini* at 24 years.

We calculated a *Paralomis*-specific COI nucleotide substitution rate using a relaxed clock analysis in BEAST 1.10 (Suchard et al. 2018). We included COI sequences from 30 *Lithodes santolla* (see Perez-Barros et al. 2015, sequences from GenBank accession numbers HM020897, HM020902, and KY426275) and the 50 *P. birsteini* sequenced here. Including such intraspecific variation should limit the elevation of inferred molecular rates that may result from ignoring ancestral polymorphisms (Peterson and Masel 2009). The divergence time of *Lithodes* and *Paralomis* is 15.2 million years (11–19 my 95% highest posterior density region, from Fig. 4 in Bracken-Grissom et al. 2013), yielding a rate of 0.00815 substitutions per site per million years or a divergence rate of 1.63%.

Results

We obtained 645 base pairs of sequence from the mitochondrial *COI* gene of the 50 *P. birsteini*. Most of the mitochondrial haplotypes were very similar to each other: two-thirds (34 of 50) shared an identical mitochondrial *COI* haplotype, with another 7 individuals just a single nucleotide substitution away (Fig. 1).

The summary statistics Tajima's D and F_s were negative, although neither was significant. R_2 , the most powerful test-statistic for recent population expansion for modest sample sizes (Ramos-Onsins and Rozas 2002), was both positive and significant. A Bayesian coalescence analysis comparing alternative models of population size positively supported the model that contained a past expansion: the natural log of the Bayes factor was 2.72 (Kass and Raftery 1995).

The coalescent reconstruction for our mtDNA data (Fig. 2) suggests that the present-day population at Marguerite Bay is significantly larger than during two periods over the last 6133 generations, the best estimate for the time to most-recent common ancestor for the

¹ <http://nucleobytes.com/4peaks/index.html>, last accessed 19/03/2019

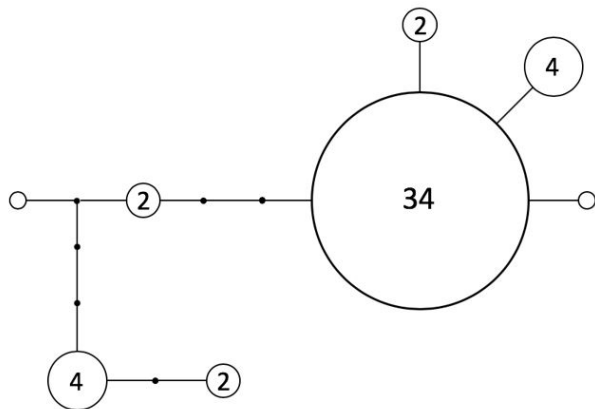


Figure 1. MtDNA variation within a population of *Paralomis birsteini* from Marguerite Bay, western Antarctic Peninsula. *COI* haplotype network for 50 individuals. The size of the open circles is proportional to the number of individuals sharing that haplotype. Haplotypes shared by more than one individual are marked with the sample size. Dots along the connecting branches represent inferred mutational steps between observed haplotypes.

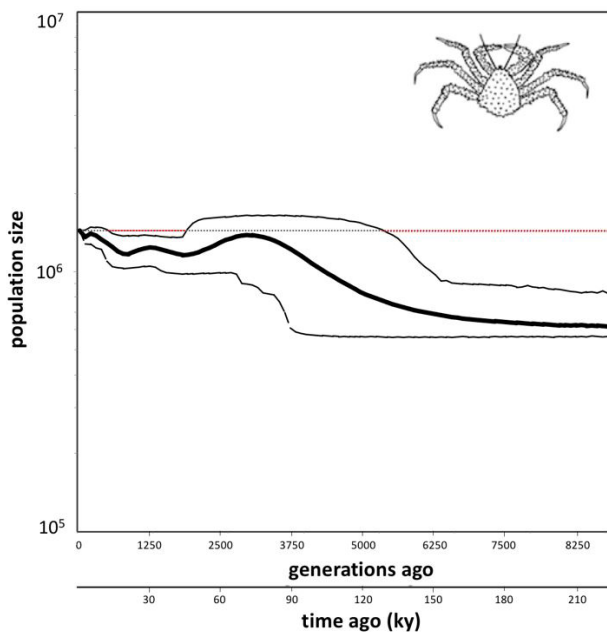


Figure 2. Inferred historical demography of *Paralomis birsteini* from Marguerite Bay. Population trajectory of *P. birsteini* inferred from GMRF skyride plot, based on mitochondrial *COI* sequences from the 50 individuals. The y-axis is plotted on a logarithmic scale. The dark central line in the plot is the mean value of effective population size through time; the dashed lines are the upper and lower 95% highest posterior densities (HPDs) for those estimates. The straight light line shows the inferred present-day population size for comparison, with the red-dashed line indicating periods when population size was significantly lower than at present.

Marguerite Bay sequences. The skyline plot (Fig. 2) shows long intervals at population sizes significantly smaller than at present but also expansion that rose to current levels about 500 and 5500 generations ago. Estimating the generation time of *P. birsteini* at 24 years, the first population expansion occurred around 132 ka and the second expansion occurred around 12 ka.

Discussion

Our findings suggest that the population of Antarctic king crabs we analyzed has undergone a demographic expansion. Most of the mitochondrial haplotypes we found are either identical or a single bp substitution apart. Values for all three summary statistics are as expected for populations that have undergone an expansion (negative for Tajima's D and Fu's F_s , positive for R_s). A model for population size with a parameter for past population growth (implemented using LAMARC, Kuhner 2006) fit our data better than one without such an expansion parameter. Finally, a GMRF skyride plot showed the past population size dropping below that of the present day twice before. Based on the taxon-specific substitution rate we calculated, past expansion occurred 132 ka, near the beginning of the last interglacial (MIS 5), and 12 ka, near the beginning of the Holocene deglaciation. Both of these climatic events were manifested as temperature increases in Antarctica (Jouzel et al. 2007) as they were elsewhere. Thus, our data align with the hypothesis that populations of *P. birsteini* experienced past population expansions that coincided with significant warming episodes in Antarctica.

Several caveats must be considered in interpreting our data, however. First, single genetic markers produce parameter-estimates with broad confidence intervals. A multi-locus analysis, coupled with species-specific information on generation times, would better constrain the times of population expansion. Second, mtDNA, like any genetic marker, may be subject to selective sweeps, and its single-locus status provides no check on this possibility. Indeed, Bazin et al. (2006) suggest that recurrent bouts of mitochondrial adaptation may blur the link between mtDNA diversity and population size, an effect that they found to be strongest in invertebrates and in the marine setting. None of the nucleotide substitutions within *COI* that we observed resulted in amino acid substitutions, but selected changes anywhere within the non-recombining mitochondrial genome could still bias our data. Nevertheless, mtDNA can successfully plot the geography of recent (post-Holocene) range expansions when multiple populations are compared (e.g., Hellberg et al. 2001, Rajabi-Maham et al. 2008). Such comparisons are presently beyond us for *P. birsteini*, however, due to a third problem. We have been able to sample only one population because of the logistical constraints of collecting from the deep sea off Antarctica. Past changes in the sampled Marguerite Bay population may not be representative of other conspecific populations, and it is possible that the signature of such changes was imported by founders that had expanded elsewhere. To resolve these issues would require a geographic survey of populations hypothesized to represent

both stable and expanded situations under the shelf invasion hypothesis. Indeed, the single mtDNA study sampling multiple king crab populations in the North Pacific was able to reveal sequential colonization from the Bering Sea down toward SE Alaska (Grant and Cheng 2012). Employing a large number of nuclear markers would increase confidence in model-selection, narrow uncertainties around parameter-estimates, and offer a means of testing for selection on mtDNA (Brumfield et al. 2003).

Although the dates of past expansions of populations of *P. birsteini* are loosely constrained given the uncertainty from both the molecular rate-estimate and the skyline plot, our data weigh against long-term population stability. The more recent expansion plausibly occurred in Antarctica; whether the earlier expansion occurred in Antarctica or elsewhere remains to be determined. This scenario provisionally puts the ascendancy of *P. birsteini* to ecological significance on the Antarctic slope within the Holocene.

Distributional data suggest that another Antarctic lithodid, *Neolithodes yaldwyni* Ahyong & Dawson, can cross regions of the shelf to populate more hospitable, deeper-water environments (Smith et al. 2012). The correlation between inferred past population expansion and climatic warming reported here suggest that king crabs may respond demographically to episodes of warmer temperatures. Together, these findings suggest that Antarctic king-crab populations should be able to respond quickly to exploit newly suitable habitats at shallower depths (Aronson et al. 2015). As the waters overlying those habitats warm rapidly, we may witness a new population expansion of *Paralomis birsteini*, with potentially important consequences for the Antarctic bottom fauna.

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Author contributions

RBA, MEH, and JBM conceived the study, with input from the other authors. KES collected the material. MEH and MID collected and analyzed the genetic data, and STA and ST supplied additional genetic data. GAL provided information on generation times. MEH and RBA wrote the paper. All authors participated in discussing and editing the manuscript.

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