

A large population of king crabs in Palmer Deep on the west Antarctic Peninsula shelf and potential invasive impacts

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Lithodid crabs (and other skeleton-crushing predators) may have been excluded from cold Antarctic continental shelf waters for more than 14 Myr. The west Antarctic Peninsula shelf is warming rapidly and has been hypothesized to be soon invaded by lithodids. A remotely operated vehicle survey in Palmer Deep, a basin 120 km onto the Antarctic shelf, revealed a large, reproductive population of lithodids, providing the first evidence that king crabs have crossed the Antarctic shelf. DNA sequencing and morphology indicate the lithodid is *Neolithodes yaldwyni* Ah Yong & Dawson, previously reported only from Ross Sea waters. We estimate a *N. yaldwyni* population density of 10 600 km⁻² and a population size of 1.55 × 10⁶ in Palmer Deep, a density similar to lithodid populations of commercial interest around Alaska and South Georgia. The lithodid occurred at depths of more than 850 m and temperatures of more than 1.4°C in Palmer Deep, and was not found in extensive surveys of the colder shelf at depths of 430–725 m. Where *N. yaldwyni* occurred, crab traces were abundant, megafaunal diversity reduced and echinoderms absent, suggesting that the crabs have major ecological impacts. Antarctic Peninsula shelf waters are warming at approximately 0.01°C yr⁻¹; if *N. yaldwyni* is currently limited by cold temperatures, it could spread up onto the shelf (400–600 m depths) within 1–2 decades. The Palmer Deep *N. yaldwyni* population provides an important model for the potential invasive impacts of crushing predators on vulnerable Antarctic shelf ecosystems.

Keywords: lithodids; invasion; Antarctic; climate warming; bioturbation; biodiversity loss

1. INTRODUCTION

It has recently been argued that lithodid crabs, and many other large durophagous (crushing) predators, have been excluded from the cold waters of the high Antarctic continental shelf (less than 600 m depths) for more than 14 Myr [1,2]. It is hypothesized that the Lithodidae have failed to colonize the Antarctic shelf due to lower thermal limits of 0.4–2°C for adults and/or larvae [1–3]. It is further speculated that the absence for millions of years of lithodids and other durophagous predators (e.g. sharks, brachyuran crabs, a variety of bony fish) from Antarctic shelf ecosystems has allowed the development of diverse epifaunal communities that are likely to be highly vulnerable to invasion by crushing predators [1,2,4].

Marine ecosystems of the west Antarctic Peninsula (WAP) are warming rapidly, with sea surface temperatures on the WAP shelf rising by approximately 1°C since 1950 [5–7]. Such warming may allow the entry of

temperature-limited taxa onto the Antarctic shelf [1]. At least 14 species of lithodids are known from the Southern Ocean north of 60° S, and significant numbers of lithodids have recently been recorded at shelf and slope depths from Antarctic Islands as far south as 67.5° S in the Bellinghousen Sea and 75° S in the Ross Sea [2,8,9]. In addition, two lithodid species (*Neolithodes capensis* and *Paralomis birsteini*) have been reported from the WAP continental slope itself, including 13 specimens (and one juvenile) of *P. birsteini* at depths of 1123–1304 m northwest of Adelaide Island (figure 1) [2,4,9]. These recent records of *N. capensis* and *P. birsteini* are hypothesized to indicate an ongoing lithodid invasion up the WAP slope and onto the shelf effected by seafloor immigration of adults or dispersal of demersal larvae [1,2]. However, the reproductive status and population densities of *N. capensis*, *P. birsteini* and other lithodids on the WAP slope are unknown (no ovigerous females have been collected on the WAP slope), and the ecosystem impacts of these and other lithodid species remain undocumented in Antarctic waters.

Here, we report the presence of an apparently large, reproductive population of the lithodid crab *Neolithodes yaldwyni* in Palmer Deep, a 1440 m deep basin on the

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Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2011.1496> or via <http://rspb.royalsocietypublishing.org>.

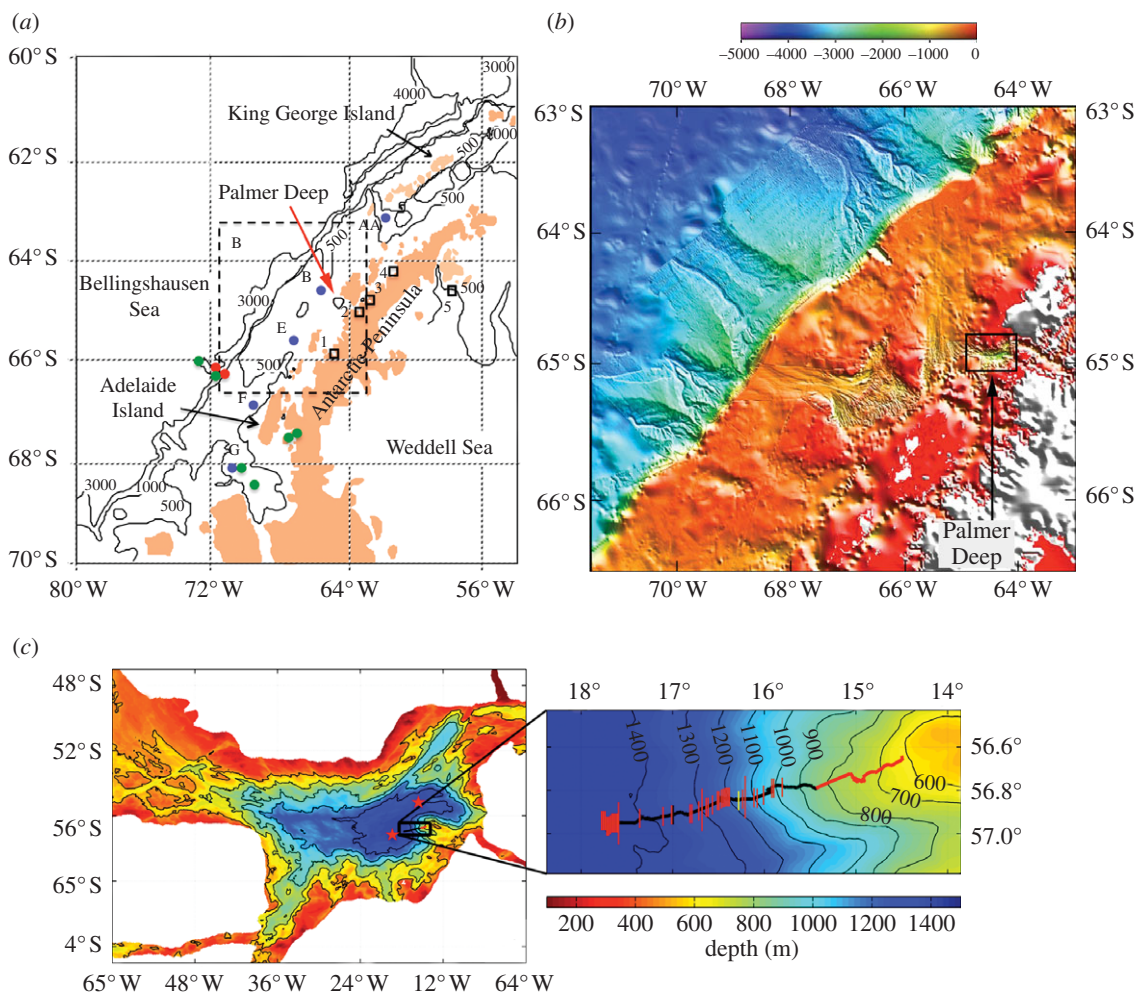


Figure 1. (a) West Antarctic Peninsula region, including Palmer Deep and stations where ROV surveys, seafloor imaging surveys and bottom trawls were conducted between 1998 and 2010. Contours are in metres. Red dots, locations where Thajte *et al.* [4] observed *Paralomis birsteinii* at depths of 1123–1304 m. Green dots, locations where Thajte *et al.* [4] failed to find lithodids during ROV surveys (depths approx. 500–600 m). Blue dots, station locations AA, B, E, F and G of trawls and yoyo camera surveys conducted in 2008–2009 during FOODBANCS2 cruises, at depths of 578–597 m, with no crabs detected (see electronic supplementary material, table S2). Boxes, locations of trawls and/or yoyo camera surveys conducted in 2010 during the LARISSA cruise at depths of 430–725 m, with no crabs detected (see electronic supplementary material, table S2). 1, Barilari Bay; 2, Flandres Bay; 3, Andvord Bay; 4, Hughes Bay; 5, Lockyer Station and Admiralty Sound. (b) Swath and GEOSAT seafloor bathymetry (depths in metres) in the vicinity of Palmer Deep (box), illustrating the typical depth (500–600 m) of the WAP shelf, and the sill depth (approx. 450 m) of Palmer Deep (bathymetric data from [10]). (c) Swath bathymetry of Palmer Deep showing ROV transect (solid black line indicates portion of transect more than 850 m, red line indicates portion of transect less than 850 m). Red vertical lines indicate positions of crabs (double length indicates crab pairs), yellow line indicates location of collected individual, black line indicates dead lithodid. Red stars, locations of seabed photographs from 1998.

inner WAP continental shelf 120 km from the open slope. This is the first evidence that lithodids can cross the Antarctic continental shelf, and the first report of *N. yaldwyni* beyond the Ross Sea. We present data on the depth distribution, ecosystem effects and evidence of reproduction for *N. yaldwyni*, based on a remotely operated vehicle (ROV) survey and crab collection. Our data indicate that this king crab has major impacts on sediment texture, bioturbation and diversity of epibenthos in Palmer Deep below 950 m, and that lithodids are likely to have been present in Palmer Deep at least since 1998.

2. STUDY AREA, MATERIALS AND METHODS

(a) Study area

Palmer Deep is a mud-floored basin located approximately 120 km southeast of the WAP continental shelf-slope break

with a maximum depth of approximately 1440 m (figure 1) [10]. The basin is approximately 14×8 km and is embedded in a continental shelf with a mean regional depth of 400–600 m (figure 1) [11]. Sedimentation rates in Palmer Deep are 0.1 – 0.4 cm yr^{-1} [12], and oxygen concentrations exceed 4 ml l^{-1} at all depths (Palmer LTER 1994–2008, unpublished data). Any water mass or planktonic larvae crossing the WAP shelf from the Southern Ocean into Palmer Deep must pass over sill depths less than or equal to 450 m on the shelf (figure 1) [10].

Water mass characteristics of the WAP shelf and Palmer Deep are complex. The top approximately 200 m of the water column is characterized by Antarctic Surface Water (AASW), which warms seasonally near the surface but remains colder than 1°C below 100 m [6,7,13,14]. Below approximately 200 m depth, the WAP shelf and Palmer Deep are influenced by Upper Circumpolar Deep

Water (UCDW), which floods and mixes eastward onto the shelf driven by the Antarctic Circumpolar Current [6,14,15]. The UCDW is typically warmer (more than 1.0°C) and more saline than the deep AASW immediately above [13]. Warming since 1990 in the WAP region is reported to have increased the heat content of the UCDW influencing the WAP shelf in the Palmer Deep region, potentially warming the upper 300 m of the UCDW by approximately 0.7°C [7].

(b) Remotely operated vehicle survey

We used *Genesis*, a *Cherokee* (Sub Atlantic) remotely operated vehicle (ROV) operated by the Renard Centre of Marine Geology, deployed from the *R/VIB N. B. Palmer* to conduct a 5.2 h survey along the floor of Palmer Deep at approximately 1419 m and up its eastern slope to a depth of 600 m (figure 1; see electronic supplementary material, table S1). Metre-scale positioning of the ROV was achieved with an IXSEA ultra-short baseline positioning (USBL) system. The ROV carried forward-looking colour digital video and digital still cameras on pan-and-tilt mountings, parallel laser scalar beams (10 cm separation), a stand-alone memory CTD (Sea & Sun Technology CTD90M; accuracy 0.005°C), a small manipulator arm and a sample drawer. The ROV was lowered to the Palmer Deep floor, and then driven eastward at approximately 0.5 knots and an altitude of 0.5–1 m (figure 1). The ROV generally moved in a straight line, occasionally stopping to obtain video and still images of megafauna and bottom features, to collect megafaunal specimens and to obtain video of crab activities. A single lithodid crab was collected by the manipulator and recovered in the ROV drawer (figure 2; see electronic supplementary material, table S1).

(c) Density estimates of crabs and other megafauna

The abundance and 95 per cent confidence limits (CL) of lithodids and other megafauna along the ROV transect were evaluated using line-transect sampling methods [16,17] and the software *DISTANCE* v. 6.2. Line-transect sampling is widely used for estimating the abundance of biological populations along linear transects, such as our ROV survey [17]. For line-transect analysis, the digital ROV video was replayed, and lithodids and other identifiable megafauna (more than or equal to 5 cm in minimum dimension) were counted as the ROV moved in a straight line at an altitude of approximately 0.5 m with good visibility; no counts were made when the ROV deviated from a linear course or when sediment was stirred up by ROV thrusters. Lithodid positions along the transect are based on GPS fixes from the ROV USBL system. The distance of each megafaunal individual from the centreline of the transect, as the animal came into ROV view, was measured using the laser scale. The ROV field of view (average 250 cm width) was also measured with the laser scale. Errors in distance measures from the centreline were estimated to be +5 cm, based on replicate measurements. We then used the program *DISTANCE* v. 6.2 to select the best model (from four alternatives) for the distribution of animals from the transect centreline based on the Akaike information criterion [17]: the *uniform key with cosine adjustments* model best fitted the crab data; the *hazard rate simple polynomial* model best fitted the non-crab megafauna. For estimates based on line-transect sampling to

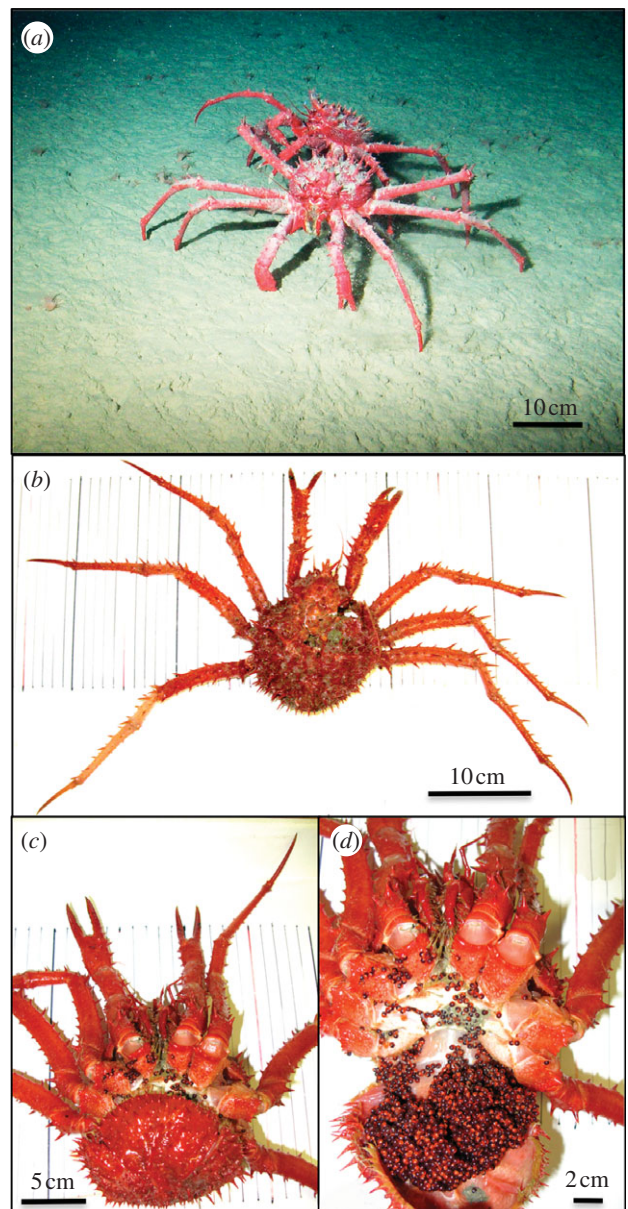


Figure 2. (a) ROV photograph of two *N. yaldwyni* at 1411 m in Palmer Deep. Crab in foreground is foraging in the sediment with its chelipeds. Note the crab traces (gashes and punctures) covering the sediment surface. (b) Dorsal view of the collected specimen of *N. yaldwyni*. (c) Ventral view of *N. yaldwyni* with brood pouch closed and (d) brood pouch open to expose developing eggs.

be unbiased, the following assumptions must be met [17]: (i) objects on the survey centreline can be detected with a probability of 1.0, (ii) objects do not move in response to the ROV prior to measurement and (iii) distances are measured with little or no error. These assumptions are reasonably well met in our dataset.

The approximate abundance of lithodid bioturbation traces on the seabed was also evaluated along the ROV survey using the laser scale. The abundance of crab bioturbation features was classified as high (more than 100 crab traces m^{-2} , with many traces overlapping), moderate (numerous isolated traces visible) or low/absent (few to no lithodid traces recognizable).

To determine whether the diversity of epifauna on drop stones differed in depth zones with abundant lithodids (i.e. at depths more than 950 m) compared with

depths without lithodid crabs (less than 850 m), we evaluated species density (i.e. number of species per unit area) on drop stones resting on the seafloor. Using the laser scale, we estimated the plan areas of drop stones visible as the ROV moved along its survey line and counted the number of distinguishable epifaunal species on each drop stone. The overlapping distribution of animals on densely covered drop stones precluded counts of individual abundance. We only included species counts for drop stones ranging in size from 200 to 1000 cm², to avoid biases resulting from the effects of drop-stone size (i.e. habitat-island area) on species diversity. Species richness per drop stone was normalized to 500 cm², the approximate mean size of drop stones studied. Differences in mean drop-stone size and species density between depth zones were assessed with *t*-tests, and differences in the proportion of 'clean' drop stones (devoid of countable epifauna) were evaluated with Fisher's exact test. Statistical tests were conducted in MINITAB v. 15. For sediment-dwelling epibenthic megafauna, diversity comparisons were made with rarefaction diversity curves for total megafauna from more than 950 m and less than 850 m, using the software PRIMER v. 6.

(d) Seabed photographs

Still photographs of the Palmer Deep seafloor were obtained in 1998 from the *RV L. M. Gould* during cruise LMG98-02, with a vertically downlooking Benthos 372 Camera and Strobe system deployed on a CTD frame with a 3 m bottom-contact switch. The bottom area photographed in each frame (5.3 m²) was calculated from camera view angles and elevation.

(e) Historical hydrographic data

Water-column profiles of *in situ* temperature and salinity for the Palmer Deep vicinity from 1980–2009 were obtained from the National Oceanographic Data Centre, from the Palmer LTER Program (courtesy of D. Martinson and R. Iannuzzi), and unpublished (but calibrated) data from cruise LMG98-02.

(f) DNA identification of the lithodid

A 650 base-pair region of the mitochondrial gene for cytochrome oxidase *c* subunit I (*COI*) was sequenced to identify the lithodid collected in Palmer Deep using accepted sequencing protocols (details provided in electronic supplementary materials). A consensus sequence was produced in SEQUENCHER v. 4.7 and compared against GenBank and the Barcode of Life databases.

3. RESULTS

(a) Lithodid abundance, depth distribution and estimated population size

The ROV survey ranged from 1419 to 600 m depths, along a total distance of approximately 3.3 km (figure 1; see electronic supplementary material, table S1). During the survey, we observed 42 live lithodid crabs and one dead specimen (or exuvium) along the 2.02 km of the survey between 1419 and 850 m depths (i.e. within the depth zone where crab traces were present; figures 1–3; see discussion of traces below). All lithodids occurred on the flat, muddy seafloor. Eighteen crabs were examined in close-up video or digital still images (e.g.

figure 2a) and they closely resembled the collected specimens in morphology and size (with carapace widths of approx. 8–10 cm); the remaining 24 crabs also resembled the collected specimen, based on visible features. Thus, all 42 observed live lithodids appear to be in the genus *Neolithodes*, and most are probably a single species, identified below as *N. yaldwyni* (figure 2). Crabs were distributed broadly along our transect below a depth of 950 m, occurring mostly as single individuals, but three times in pairs within 2 m of one another. We estimate crab abundance within the 850–1419 m depth range to be 10 600 km⁻² (95% CLs 8030–13 900 km⁻²), based on line-transect sampling [16] (table 1). The area of Palmer Deep below 950 m (i.e. the depth zone where crabs and crab traces were most abundant) is 146 km²; if we assume that the mean abundance (95% CL) of crabs per km² on our transect are representative of the entire Palmer Deep area below 950 m, then this yields a *N. yaldwyni* population size of 1.55×10^6 individuals within Palmer Deep (95% CL of 1.17 to 2.04×10^6).

(b) Lithodid identification

A single ovigerous female crab (carapace width = 103.6 mm, carapace length = 117.3 mm, postorbital carapace length = 103.2 mm), carrying nearly mature eggs and larvae, was collected at a depth of 1154 m (figure 2; see electronic supplementary material, table S1). A 650 nucleotide region of the *COI* gene for this female specimen was identical to *COI* sequences of two *N. yaldwyni* specimens identified by S. Ah Yong, a co-describer of the species [18] (see electronic supplementary material, figure S1). The Palmer Deep *N. yaldwyni* *COI* sequences are substantially distinct from those of the closely related species *N. brodiei*, *N. asperrimus* and *N. duhameli* (see electronic supplementary material, figure S1). Morphologically, the collected specimen keys out to *N. yaldwyni* [19] and matches the diagnosis of *N. yaldwyni* [18,19]. We are therefore confident that this gravid female is *N. yaldwyni*.

(c) Lithodid locomotion, feeding and bioturbation

Numerous king crabs were observed walking across the Palmer Deep seafloor, creating puncture marks with leg tips and gashes in the sediment as leg tips were dragged through the sediment (figures 2 and 3; see electronic supplementary material, videos S1 and S2). Puncture marks from leg tips were approximately 1 cm in diameter and gashes were up to approximately 1 cm wide, approximately 0.5 cm deep and up to 20 cm long. In addition, crabs were observed to forage by repeatedly probing the sediment to 3–4 cm depths with open chelipeds, closing the chelipeds while the tips were submerged in the sediment, and then scooping the captured sediment bolus into open mouthparts for processing (figure 2a; see electronic supplementary material, videos S1 and S2). This probing and scooping activity created sediment puncture marks and clumps 2–3 cm across (figure 3). Much of the sediment scooped to the mouthparts fell through the mouthparts during processing (see electronic supplementary material, video S1). This locomotion and foraging activity created a dense fabric of gashes, punctures and sediment clumps, producing a characteristic gashed/lumpy texture to the sediment–water interface (figures 2a and 3). The crab

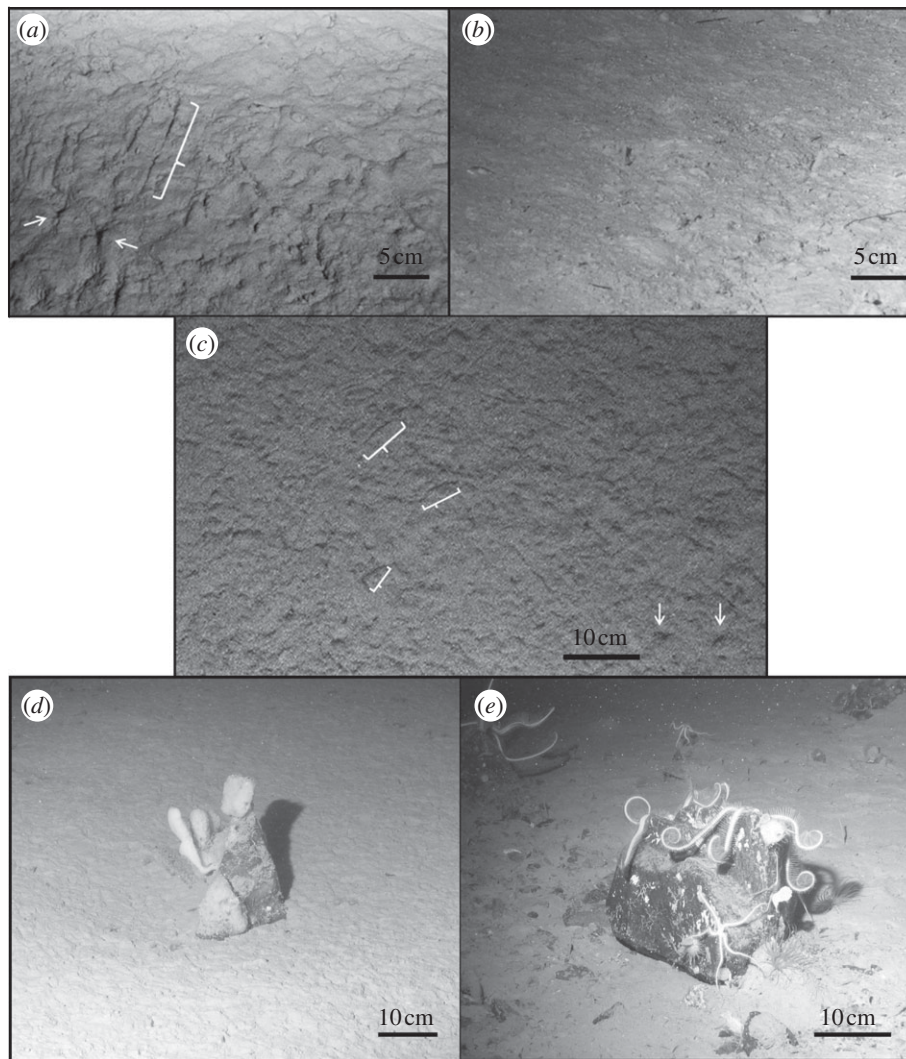


Figure 3. (a) ROV photograph of *N. yaldwyni* traces in seafloor sediments at 1418 m depth in Palmer Deep. Brackets, gashes in sediment formed by *N. yaldwyni* walking. Arrows, paired puncture marks and clumps formed during lithodid foraging in the sediment with chelipeds (see figure 2a; see electronic supplementary material, videos S1 and S2). Note that fresh traces cross over older traces. (b) Palmer Deep seafloor at 836 m depth, illustrating the absence of *N. yaldwyni* traces. (c) Vertical photograph of Palmer Deep seafloor at 1425 m in 1998 (southern red star in figure 1c). Brackets, apparent lithodid walking gashes (straight and V-shaped); arrows, puncture marks and sediment clumps similar to those formed during lithodid foraging. (d) Example of a drop stone from the *N. yaldwyni* depth zone (more than 950 m) with only hexactinellid sponges and serpulid worm tubes visible (1360 m). Note crab traces in the sediments around the stone. (e) Example of a drop stone from above the *N. yaldwyni* depth zone (less than 850 m), with brisingid asteroids, ophiuroids, an echinoid, hexactinellid sponges and serpulid worm tubes visible (811 m).

Table 1. Estimated population densities (and 95% CLs) for *N. yaldwyni* and other (non-crab) sediment-dwelling epibenthic megafauna along the ROV transect in Palmer Deep. *Neolithodes yaldwyni* density was calculated over the depth interval where crabs were observed and crab bioturbation traces evident (850–1419 m). Densities of other sediment dwelling megafauna were calculated for depths of more than 950 m (*N. yaldwyni* present and crab traces abundant) and less than 850 m (*N. yaldwyni* and crab traces absent) to evaluate lithodid influence.

taxon	depth zone (m)	density (km^{-2})	lower 95% CL (km^{-2})	upper 95% CL (km^{-2})
<i>Neolithodes yaldwyni</i>	>850 (850–1419)	10 600	8030	13 900
cerianthid anemones	<850 (600–850)	15 000	3710	60 500
cerianthid anemones	>950 (950–1419)	47 800	43 300	52 700
non-crab megabenthos without cerianthid anemones	<850 (600–850)	4670	^a	^a
non-crab megabenthos without cerianthid anemones	>950 (950–1419)	4290	3070	6010

^aSample size too small to calculate CLs.

locomotion and foraging activities in Palmer Deep appeared to substantially mix sediments to depths of 3–4 cm.

The abundance of lithodid walking and feeding traces was high (approx. 100–300 lithodid traces per m^2) and the gashed/lumpy sediment texture was continuous from

depths of 1419 to approximately 950 m along the transect (figures 2a and 3). From depths of approximately 950 m to approximately 850 m, the lithodid trace abundance gradually diminished from high to low/absent until there was no evidence of crab activity on the sediment shallower than approximately 850 m (figure 3). At depths of less than 850 m, the texture of soft sediments was relatively smooth, and characterized by worm tubes and small biogenic mounds (features missing at depths more than 950 m), indicating that walking and foraging *N. yaldwyni* were rare or absent shallower than approximately 850 m in Palmer Deep (figure 3). At depths of 850–600 m in Palmer Deep, sediment texture and bioturbation features were similar to those of the muddy seafloor observed over wide areas of the WAP shelf at depths of 430–725 m at latitudes from 63 to 68° S, where lithodid crabs have not been recorded during extensive bottom photographic surveys and trawl sampling (figure 1; see electronic supplementary material, table S2; [20]; C. R. S. Smith, L. J. Grange & C. Clark 2008–2010, unpublished data).

All three photographs of the Palmer Deep floor from 1998 (cruise LMG98-02), taken at two locations 1–4 km from the ROV transect (figure 1), show a sediment surface covered with a gashed/lumpy texture (figure 3). This sediment surface texture is essentially identical to that along the ROV transect between depths of 1419 and 950 m (figure 3), and suggests that foraging lithodids were present at approximately 1400 m depths in Palmer Deep in 1998, 12 years prior to our ROV survey. Although no crabs were observed in the photographs, at the density of crabs estimated from our ROV survey (approx. 0.01 m^{-2}), the probability of seeing a lithodid in three photographs covering a total area of approximately 16 m^2 was very small (less than 2%).

(d) Abundance and diversity of other benthic megafauna

The abundance of sediment-dwelling, epibenthic megafauna countable in the ROV video was approximately threefold greater within the crab zone at depths more than 950 m than at depths without crabs (i.e. less than 850 m; table 1); however, 90 per cent of megafaunal abundance at depths of more than 950 m consisted of a single species of cerianthid anemone, while cerianthids constituted 76 per cent of abundance at depths of less than 850 m. The abundance of non-cerianthid, sediment-dwelling megafauna was thus roughly similar at depths of more than 950 m and less than 850 m (approx. 4290 km^{-2} and approx. 4670 km^{-2} , respectively; table 1). Rarefaction diversity of the sediment-dwelling megafauna was substantially higher at depths of less than 850 m than at depths of more than 950 m (figure 4). This was a consequence of both greater taxonomic richness (curve endpoints) and much greater evenness (initial curve slopes) at the shallower depths (less than 850 m) where *N. yaldwyni* was absent. Echinoderms were absent from the sediment-dwelling epibenthic megafauna at depths of more than 950 m, while four species of echinoderm (three asteroids and a cidaroid urchin) occurred on sediments at depths of less than 850 m. Two species of demersal fishes (a nototheniid and a zoarcid) occurred on sediments at depths of more than 950 m, and only the nototheniid species occurred

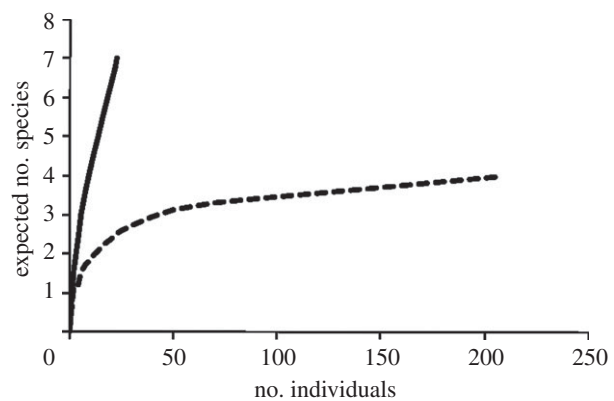


Figure 4. Rarefaction diversity curves for the sediment-dwelling megafauna in Palmer Deep at depths of more than 950 m (where *N. yaldwyni* and its traces were abundant; dashed line) and less than 850 m (where *N. yaldwyni* and its traces were absent; solid line).

at depths of less than 850 m. Fish densities were higher at more than 950 m than at less than 850 m depths (3700 versus 1900 km^{-2}), but small sample sizes ($n = 20$ and 1 , respectively) precluded statistical significance using line-transect analysis.

Species richness and species density of epifauna on drop stones was substantially higher, and the percentage of clean drop stones substantially lower, at depths of less than 850 m (i.e. above the depth zone of *N. yaldwyni*) than within the lithodid depth zone at depths of more than 950 m in Palmer Deep (figure 3, table 2). In particular, mean species density (i.e. number of species per 500 cm^2) was fourfold lower (two-sample *t*-test, $p = 0.006$), and the percentage of drop stones devoid of epifauna 3.5-fold higher (Fisher's exact test, $p < 0.003$), in the presence of *N. yaldwyni*. Echinoderms were wholly absent from drop stones at depths of more than 950 m, while four species (a brisingid asteroid, two species of ophiuroids and an echinoid) occurred on drop stones at depths of less than 850 m.

(e) Palmer Deep hydrography

During the ROV dive, *in situ* seafloor temperatures declined from 1.53°C at 1419 m depth to 1.45°C at 600 m (figure 5). Since the lithodid and its traces disappeared at depths of less than 850 m, *N. yaldwyni* appeared to be restricted to water temperatures more than or equal to 1.48°C within Palmer Deep.

Bottom temperatures in Palmer Deep have exhibited a warming trend from 1982 to 2010, with the temperature minimum increasing from 1.20°C to 1.47°C below 800 m depths (i.e. increasing at a rate of approximately $0.01^\circ\text{C yr}^{-1}$; figure 5). In 1998, when crab traces were present, the Palmer Deep bottom temperature was approximately 1.4°C . During the time interval 1990–2005, composite summer and winter hydrographic sections across the WAP shelf into Palmer Deep suggest that benthic or larval stages of lithodids dispersing near the seafloor across the sill depth of approximately 450 m into Palmer Deep would probably have experienced temperatures no colder than approximately 1.0°C (figure 5; see electronic supplementary material, figure S2). Minimum temperatures within the depth range of 400–600 m in Palmer Deep (i.e. at the mean depth of

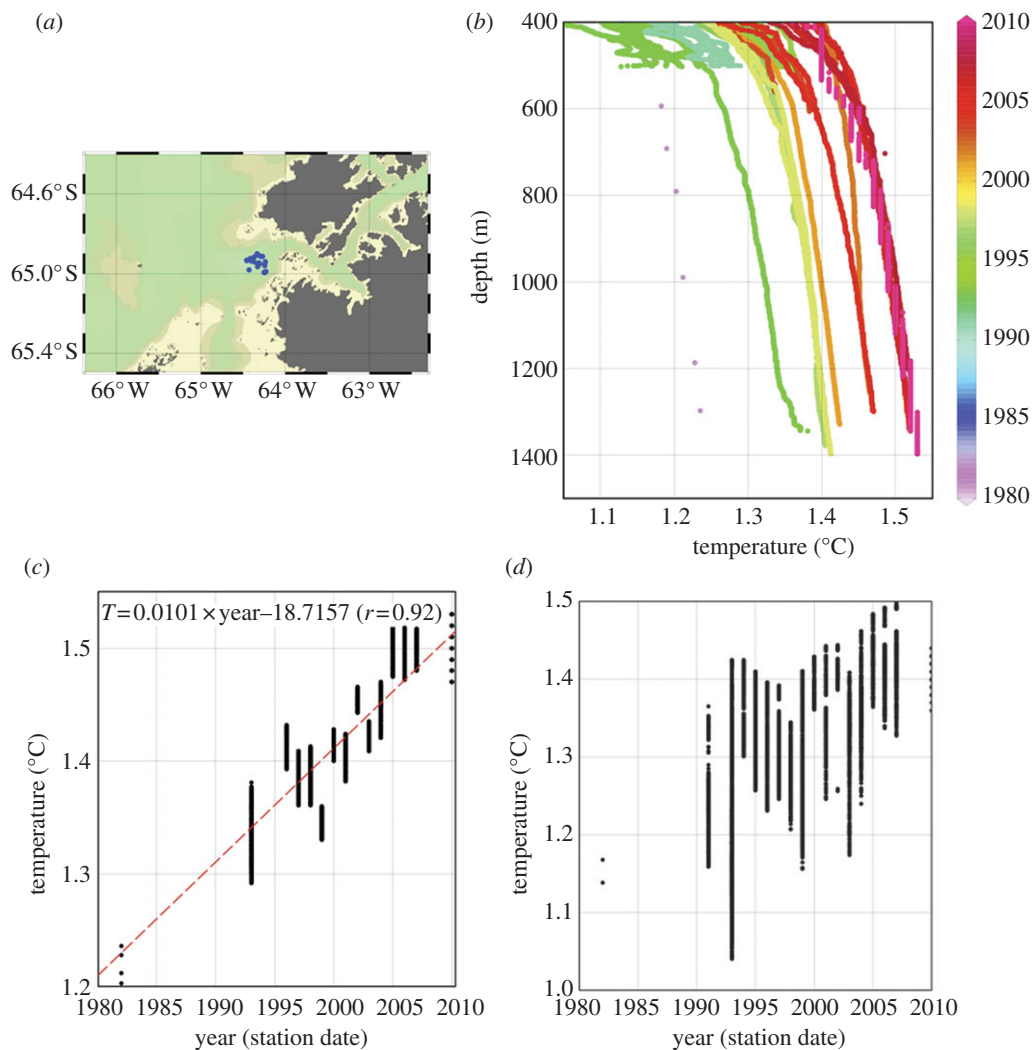


Figure 5. Temperature-profile data from Palmer Deep from 1982 to 2010. (a) Locations of hydrographic profiles indicated by blue dots. (b) Profiles of *in situ* water temperature versus depth in Palmer Deep. Colours (see scale bar) indicate time of data collection. (c) *In situ* water temperature over the 800–1400 m depth interval versus time in Palmer Deep. The linear regression equation at the top indicates a warming trend of approximately $0.01^{\circ}\text{C yr}^{-1}$. (d) *In situ* water temperature over the 400–600 m depth interval in Palmer Deep versus time.

Table 2. Mean size and epifaunal species diversity for drop stones $200\text{--}1000\text{ cm}^2$ in plan area at depths $>950\text{ m}$ (*N. yaldwyni* and crab traces abundant) and $<850\text{ m}$ (*N. yaldwyni* and crab traces absent) in Palmer Deep. ‘Clean’ drop stones had no identifiable epifauna. s.e., standard error.

depth zone (m)	no. of stones	mean stone plan area (cm^{-2})	s.e.	total no. of species in zone	mean species density (per 500 cm^{-2})	s.e.	proportion of clean drop stones
>950 (950–1419)	33	478	35	8	0.488	0.142	0.64
<850 (600–850)	17	493	40	14	2.09	0.505	0.18

the continental shelf in the region; figure 1) exhibit substantial seasonal and inter-annual variability, but appear to have risen from approximately 1.04 to 1.36°C since 1992 (i.e. at a rate of approximately $0.01\text{--}0.02^{\circ}\text{C yr}^{-1}$; figure 5).

4. DISCUSSION

Our ROV survey indicates that large, adult lithodids, most probably *N. yaldwyni*, were abundant over large areas of the Palmer Deep seafloor at depths of 950–1419 m in February 2010. The population density of *N.*

yaldwyni estimated for Palmer Deep ($10\,600\text{ km}^{-2}$, 95% CL of $8030\text{--}13\,900\text{ km}^{-2}$) is greater than the mean density (5100 km^{-2}) of the commercially important red king crab *Paralithodes camtschaticus* in an Alaskan fjord, and similar to the abundance of the lithodid *Paralomis formosa* being considered for commercial exploitation at depths of 719–1518 m on the South Georgia slope (mean = 8313 km^{-2}) [21]. The biomass of *N. yaldwyni* in Palmer Deep is also potentially large; if we apply the lithodid body-weight model of Collins *et al.* [21] to adult *N. yaldwyni*, each *N. yaldwyni* has a weight of approximately 500 g, yielding an estimated crab biomass in Palmer

Deep of approximately 5000 kg km^{-2} . Our ROV transect only crossed a portion of the Palmer Deep seafloor deeper than 950 m, but king crabs and crab traces were broadly distributed along this approximately 2 km transect; if we assume that the estimated *N. yaldwyni* abundance was representative of the entire Palmer Deep more than 950 m in depth, the population size of *N. yaldwyni* in Palmer Deep exceeded 1.55×10^6 individuals and the biomass was substantial (approx. 800 tonnes).

Some lithodids are known to aggregate during certain life stages [21,22]. Is it conceivable that the high densities of *N. yaldwyni* recorded along the ROV transect reflect a recent lithodid aggregation in the process of dispersing? The broad distribution of lithodids and abundant crab traces throughout our approximately 2 km ROV transect below 950 m, as well as the abundance of traces in widely spaced bottom photographs from 1998, are not consistent with an aggregation in the process of dispersing. Thus, we think it very probable that lithodids are broadly dispersed across the floor of Palmer Deep below 950 m.

There is evidence that *N. yaldwyni* exerts substantial impacts on bioturbation, ichnofabric, and the diversity and taxonomic structure of megabenthos in Palmer Deep. Walking and feeding activities of lithodids in Palmer Deep created a high abundance of traces and a gashed/lumpy sediment texture covering the seafloor at depths of more than 950 m (figures 2a and 3; see electronic supplementary material, videos S1 and S2). This gashed/lumpy texture closely resembles the sediment texture of 'digging pits and tracks' created by invasive red king crabs (*Paralithodes camtschaticus*) in the Barents Sea in the Arctic [23]. We cannot directly calculate a bioturbation rate from the activities of *N. yaldwyni* in Palmer Deep, but the sedimentation rate of approximately $0.1\text{--}0.4 \text{ cm yr}^{-1}$ [12] indicates that the centimetre-scale lithodid traces should be obscured by sediment accumulation (i.e. buried beneath 0.5–1.0 cm of sediment) in less than 10 years. In addition, the fresh appearance and overlap of many lithodid traces (figures 2a and 3; see electronic supplementary material, videos S1 and S2) indicate that crab retracking is causing trace turnover at much shorter timescales than sediment accumulation [24]. Thus, the heavy cover of lithodid traces at depths of more than 950 m (figure 3) suggests that the particle-displacement and predatory activities of king crabs are influencing much of the sediment to depths of 1–4 cm over timescales much less than 10 years. Other studies have shown that the walking, resting and foraging activities of epifaunal crabs (including lithodids) can mix surface sediments to depths of several centimetres [25], disrupt infaunal tubes and burrows (i.e. alter ichnofabric), and change rates and patterns of bio-irrigation by removing infauna performing important ecosystem functions [23,26]. Thus, *N. yaldwyni* is likely to be acting as a major ecosystem engineer [26,27] by substantially modifying the bioturbation regime, sediment stratigraphy and sediment geochemistry (e.g. the location of labile organic matter decomposition and the depth of the redox potential discontinuity of Palmer Deep sediments), and by removing habitat-forming echinoderms (see below). These sedimentological alterations could prove useful for reconstructing the history of king crabs in Palmer Deep from sediment stratigraphy.

The diversity of epibenthic megafauna, both on sediments and on drop stones, was substantially lower in

the lithodid depth zone (more than 950 m) than at depths lacking lithodids in Palmer Deep (less than 850 m). In particular, echinoderms, which are common prey items for lithodids [1,26], were absent on soft sediments and drop stones within the lithodid depth zone, yielding substantial declines in biodiversity. Megafauna on sediments and on drop stones were dominated by tubicolous cerianthid anemones and sponges, respectively; both these taxa appear to be lightly preyed upon by lithodids in other regions [26]. The diversity and taxonomic structure of megabenthos in the Palmer Deep lithodid zone was also markedly different from similar depths on the nearby open slope lacking crabs; in photosurveys at 800–1000 m depths off King George Island, Piepenburg *et al.* [28] found no lithodids, relatively high megafaunal diversity (17–24 species versus 8 in our Palmer Deep data) and abundant echinoderms ($3.8\text{--}6.0 \text{ m}^{-2}$). These data are highly consistent with the hypothesis that predation by the duraphagous predator *N. yaldwyni* reduces the diversity and alters the community structure of Antarctic megabenthos below depths of 950 m in Palmer Deep, as predicted for lithodid invasions of Antarctic communities [1,2,4]. Similar substantial reductions in epifaunal diversity have been associated with king crab invasions in Arctic fjords [23,26]. Nonetheless, because our results on the impacts of *N. yaldwyni* on benthic diversity in Palmer Deep are correlative, they need to be confirmed by additional studies (e.g. gut-content and biomarker analyses, and crab-exclusion experiments).

Based on our ROV survey, *N. yaldwyni* and its traces were absent from depths of less than 850 m in Palmer Deep. Extensive photographic and trawl surveys from 2008–2010 at nineteen stations at depths of 430–725 m along the WAP shelf and in fjord basins from 63° to 68° S also failed to detect lithodids or their traces (figure 1; see electronic supplementary material, table S2). The total area surveyed and trawled (approx. $238\,000 \text{ m}^2$) at the nineteen stations is approximately 40-fold greater than the area surveyed by the ROV in Palmer Deep, providing strong evidence that *N. yaldwyni* or other lithodids did not occur at depths shallower than 725 m on muddy habitats on the WAP shelf from 2008 to 2010. Similarly, Thatje *et al.* [4] failed to find lithodids on the continental shelf at depths of 500–600 m in Marguerite Bay in 2007, and extensive video and trawl surveys of the WAP shelf west of Palmer Deep at depths of 500–600 m failed to detect lithodids between 1999 and 2001 [11,20]. We conclude that lithodid crabs, including *N. yaldwyni*, were absent or extremely rare on the WAP shelf at depths of less than 725 m at least up to 2010. It is noteworthy that megabenthic abundance and diversity in these lithodid-free, soft-sediment WAP communities at 430–725 m depths were dominated by echinoderms, which are absent from the lithodid zone in Palmer Deep ([20]; C. R. S. Smith, L. J. Grange & C. Clark 2008–2010, unpublished data).

The abundance, large body sizes, apparent isolation and extensive bioturbation effects of *N. yaldwyni* in Palmer Deep suggest that this population had been established for years. The abundance of apparent crab traces at the Palmer Deep floor in 1998, 12 years prior to our ROV survey, is consistent with this conclusion. It seems unlikely that *N. yaldwyni* in Palmer Deep is maintained by continuous migration of walking life stages across the shelf because of the apparent absence of benthic life

stages from the shallower depths surrounding Palmer Deep over the period 1999–2010 (see electronic supplementary material, table S2) [20]. Similarly, the poor dispersal abilities of demersal, lecithotrophic lithodid larvae [29,30] suggest that continuous transport of *N. yaldwyni* larvae over distances more than 120 km across the shelf is unlikely. The recovery of an ovigerous *N. yaldwyni* female from Palmer Deep indicates that this lithodid population is capable of reproduction; thus, the population may be self-sustaining. Alternatively, the high abundance of king crabs in Palmer Deep could have resulted from one or a few large recruitment events mediated by benthic immigration, or, perhaps more probably, by pulsed larval transport from the continental slope across the shelf in UCDW [14]. Demographic, reproduction and genetic studies of the Palmer Deep *N. yaldwyni* population are needed to resolve its occupation history.

The abundance of *N. yaldwyni* in Palmer Deep below 950 m, and its apparent absence at depths of less than 850 m and water temperatures below 1.4°C, has interesting implications for the invasion of WAP shelf waters by this species. If the distribution of lithodids in Antarctic waters is limited by a lower temperature threshold, as argued by a number of authors [1–4], our results suggest that the Palmer Deep population of *N. yaldwyni* cannot disperse and/or reproduce in temperatures colder than approximately 1.4°C. In 1982, Palmer Deep bottom temperatures were significantly colder than 1.4°C, at approximately 1.25°C (figure 5), and were likely to have been warming for some decades [5]; thus a lower temperature limit of approximately 1.4°C would suggest that *N. yaldwyni* invaded Palmer Deep within the last approximately 50 years. A lower limit of 1.4°C is significantly warmer than the 0.5°C waters from which individual adult *N. yaldwyni* have been reported from the Ross Sea [2,19], so different populations of *N. yaldwyni* may have different temperature tolerances. Alternatively, other unknown environmental factors might exclude *N. yaldwyni* from depths of less than 850 m in Palmer Deep; however, fish predation on crab larvae and juveniles [26] is unlikely to be important since demersal fishes are, if anything, more abundant in the lithodid zone of Palmer Deep than just above. If temperatures of less than 1.4°C are indeed limiting for the Palmer Deep population, *N. yaldwyni* may not long be excluded from the WAP shelf. Considering the rate at which Palmer Deep waters are warming (approx. 0.01°C yr⁻¹) and the fact that WAP shelf waters (i.e. at 400–600 m depths) around Palmer Deep now have temperature minima around 1.35°C (figure 5; see electronic supplementary material, figure S2), the Palmer Deep *N. yaldwyni* could move up onto the WAP shelf within 1–2 decades. Thus, the population size, depth distribution and ecological impacts of the Palmer Deep *N. yaldwyni* population merit careful study in the near future to elucidate the rates and consequences of WAP shelf invasion by durophagous lithodid predators. The Palmer Deep lithodid population is likely to serve as an important model for the potential invasive impacts of crushing predators, especially king crabs, on Antarctic shelf ecosystems due to climate warming.

We are very grateful to the extraordinary support at sea provided by RPSC, the captain and crew of the *R/VIB*

N. B. Palmer, and our colleagues in the LARISSA Project during cruise NBP10-01. Data collection occurred as parts of the LARISSA and FOODBANCS2 Projects, and was generously supported by NSF-OPP grant numbers 0732711 and 0636806 to C.R.S., 0732467 to E.D., 0732450 to C. L. Van Dover and 074735 to B.H. The ROV was funded by Impulsfinanciering of the Special Research Fund of Ghent University, and participation of the ROV team (Dries Boone, Katrien Heirman and Lieven Naudts) was co-financed by the BELSPO project HOLANT. We thank the referees A. Clarke, H. Ducklow and J. Pearse for substantially improving the manuscript. This is publication number 8479 from SOEST, University of Hawaii at Manoa and number 7492 from Lamont-Doherty Earth Observatory.

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