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***Antarctic Lithodids (King Crabs): Climate Change and  
Threats to Antarctic Marine Ecosystems***

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**Abstract**

Anthropogenic climate change resulting in warming of global oceanic temperatures will likely allow the entry of previously temperature-limited taxa onto the Antarctic shelf. Indigenous Antarctic shelf benthos have evolved in isolation for millennia with the absence of durophagous (shell crushing) predators a significant factor in their 'archaic' Paleozoic character. The potential consequences of an invasion by lithodids could have a devastating effect on the Antarctic shelf benthos, homogenising the ecosystem, contributing to the diminished global diversity of marine ecosystems. 14 species of invasive crab have already been recorded in Antarctic waters in previously unknown locations. Polar regions are considered particularly vulnerable in a changing climate and at risk from potential invasive species.

# **Antarctic Lithodids (King Crabs): Climate Change and Threats to Antarctic Marine Ecosystems**

## **Introduction**

The vulnerability of polar benthic ecosystems to invasion from species extending their range due to the anthropogenic climate change is widely accepted, and is likely to increase and become exacerbated in the coming decades as mean sea level temperatures increase (Thatje et al., 2005a, Smith et al., 2012). The Antarctic Circumpolar Current (ACC) has kept the Antarctic continental shelf waters cooler than the deeper surrounding waters, creating a thermal barrier between ecosystems and excluding durophagous shell crushing predators from the shelf for millennia (Aronson et al. 2015b). Sea temperatures around Antarctica are increasing as anthropogenic climate change continues, the thermal barriers between ecosystems are disappearing and Antarctic shelf waters are now within the tolerance levels of the previously excluded Antarctic King Crabs (family *Lithodidae*), posing a significant threat to Antarctic shelf benthos (Aronson et al., 2015b, Smith et al., 2012). Decapod diversity in the Antarctic is low compared with the sub-Antarctic (Wittmann et al., 2010). Consequently, isopods and amphipods occupy ecological niches in Antarctic shelf benthos typically occupied by crabs at higher latitudes (Wittmann et al., 2010). The biogeography of decapod species can therefore to some extent be explained by limitations in their magnesium regulation pathways (Wittmann et al., 2010, Thatje et al., 2005a). Previously temperature-limited taxa are 'invading' the Antarctic shelf (Smith et al., 2012) with potential homogenising impacts on indigenous benthic communities and further contributing to the diminished global diversity of marine ecosystems (Aronson et al., 2015b).

## **Susceptibility of the polar regions to invasive species**

Aronson et al. (2015a) have argued that polar regions in the past have been "physically resistant to biological introductions and range expansions" (Aronson et al., 2015a, p. 1) due to their colder temperatures. In a warming climate however, polar regions are becoming more susceptible to invasion with cooler temperatures that previously created physiological barriers, becoming increasingly permeable and eroded (Thatje et al., 2005b). These barriers to invasion are now being threatened as sea temperatures rise and thermal tolerances become less of an issue with potentially devastating and homogenising effects for the Antarctic shelf marine benthos. The intense

seasonality and cold temperature adaptations of taxa specific to polar regions make these areas particularly at risk and vulnerable to climate change (Aronson et al. 2007), in particularly influencing the presence of higher level predators.

### **Antarctic Shelf benthos**

Mean global sea temperatures have been declining for the past 50 million years leading to dramatic changes in Antarctic marine ecosystems including “the loss of major taxonomic groups such as pelagic and benthic top predators... and a reduction in the biodiversity of [taxonomic] groups, such as bivalve molluscs, teleost fishes and decapods” (Thatje, Hillenbrand & Larter, 2005, p. 535). The endemic taxa of the shallow Antarctic shelf communities consequently reflect Palaeozoic fauna (Aronson et al., 2015b, Thatje et al., 2005b). The evolutionary historical lack of ‘higher’ durophagous (shell crushing) predators, such as teleost fish, crabs and sharks (Clarke et al., 2005) is significant in determining the present structure and function of these modern archaic fauna (Aronson et al., 2007). The Antarctic shelf marine benthos species exhibit a high level of endemism that is typically associated with an evolutionary history in isolation (Aronson et al., 2007, Clarke et al., 2005), with the onset of the Antarctic Circumpolar Current crucial to speciation events in the region post Eocene (Aronson et al., 2007, Clarke et al., 2005). As a result of this evolutionary history in isolation, the benthic fauna of the Antarctic shelf are lightly skeletonised, lacking defensive structures and behaviours leaving them particularly vulnerable to an invasion by durophagous predators (Aronson et al., 2015a, Clarke et al., 2004). Presently, the top predators are slow moving invertebrates such as echinoderms (Aronson et al., 2015a). The benthic communities in the Antarctic are dominated by epifaunal suspension feeders (Clarke et al., 2004).

### **The Antarctic Circumpolar Current and Sea Temperature**

The Antarctic circumpolar current (ACC) is considered a physiological barrier to invasive species in Antarctic waters (Clark et al., 2004, Aronson et al., 2015a). With the exception of migratory birds and some of the larger macro fauna, there are few species that occur both within and outside the Southern Ocean (Aronson et al., 2007, Clarke et al., 2005). However, Aronson et al. (2007) and Thatje et al. (2005a) have suggested the barrier provided by the ACC is more permeable than initially thought and increasingly complex. Taxa that have a pelagic (inhabiting the water column) larval stage, may have an advantage in their ability to “(re)colonise” the Antarctic by passing through the ACC (Thatje et al., 2005b). The importance of oceanographic features such as eddies in

transporting species to Antarctica through the ACC is widely discussed but the frequency with which such events take place largely unknown (Aronson et al., 2007, Thatje et al., 2005b). The presence of the ACC is crucial in determining the absence of durophagous (shell-crushing) predators from Antarctic shelf benthic ecosystems by creating a thermal divide between the shelf waters and the deeper warmer waters beyond (Aronson et al., 2015b). As a result these Antarctic shelf ecosystems are often described as Paleozoic in structure (Aronson et al., 2007, Aronson et al., 2015b) with the top predators being very slow moving species such as echinoderms and amphipods (Aronson et al., 2015a,b, Clarke et al., 2004).

Over the past ~50 million years mean global oceanic temperatures have experienced a long period of cooling (Thatje et al., 2005b). However, anthropogenic climate change is at present, warming the world's oceans at an alarming rate, with the 'isolated' polar regions unable to escape the negative impacts of human activity (Aronson et al., 2011, Bennett et al., 2015, Hall & Thatje, 2011, Clarke et al., 2005). "Antarctic shelf bottom waters off the WAP have risen by nearly 1.5°C over the past 50 years, approximately double the globally averaged rate" Aronson et al., 2015a, p. 12998). As the shallow WAP water temperatures increase, the thermal barrier to invasion by lithodids will gradually be removed, aiding their spread into Antarctic shelf benthic communities (Aronson et al., 2015a, Thatje et al., 2005a).

### **Thermal tolerance**

Decapod diversity is low in Antarctic shelf communities compared to continental shelf waters in temperate regions (Thatje et al., 2005a). The amount of shelf habitat available during phases of ice retreat and expansion would have varied significantly limiting the biodiversity on the Antarctic shelf with localised and regional extinctions (Thatje et al., 2005b). Temperature has long been a limiting factor for taxa on the Antarctic shelf (Smith et al., 2012) with the barriers to invasion considered physiological rather than geographical (Aronson et al., 2007, Thatje et al., 2005). Lecithotrophy (non-feeding developmental mode, relying on origin material (Thatje et al., 2005b)) in larvae stages of the life cycle and  $Mg^{2+}$  regulation are both significant factors in determining why crabs have remained excluded from high Antarctic and Arctic ecosystems and how they beginning to extend their range. Adaptations to the cold and to deep sea require similar evolutionary adaptations, with the ability to down regulate  $Mg^{2+}$ , an important oxygen supply mechanism for life in cold water (Thatje et al., 2005). It is hypothesised that lithodid crabs have been excluded from Antarctic shelf waters for 10-25 million years during which time climatic conditions experienced significant cooling. Decapod species that thrive in cold waters have the ability to efficiently down

regulate  $Mg^{2+}$  such as in shrimp and isopods and these organisms consequently experience relative levels of abundance in the Antarctic (Wittmann et al., 2010). In brachyuran and anomuran crab species however, this ability is hindered and considered a contributing factor in the absence of such species from polar waters for millennia (Aronson et al., 2015b, Thatje et al., 2005a). Wittmann et al. (2010) associate a life history of deep sea adaption as playing a significant role in the success of lithodidae and other associated taxa in their colonisation of the Antarctic Peninsula region in 'recent' times. In 2010, Wittmann et al. confirmed previously held assumptions concluding that lithodid crabs are "rather poor haemolymph magnesium regulators and do not thrive in waters colder than 0°C" (Wittmann et al., 2010, p. 926). Consequently, thermal tolerances of other adjacent benthic species could provide a useful indication of future 'invasiveness' (Aronson et al., 2015b, Aronson et al., 2007, Wittmann et al., 2010).

### Crab Invasion

Reptant (bottom-dwelling, walking decapods) durophagous crabs have been excluded from the Antarctic for millennia. However, in recent years, numerous species have been discovered further south than previously recorded with the scale of potential invasive impacts on Antarctic benthic ecosystems of great concern, but yet to be determined. In 1986 the Atlantic spider crab, *Hyas araneus*, was recorded on the Western Antarctic Peninsula off King George Island (Tavares & De Melo, 2004) representing the first indication of an invasion of predatory species in the Antarctic benthos (Aronson et al., 2007). *H. araneus* is a north Atlantic species and could only have been introduced to the Antarctic "via the transport of adults on ships' hulls or larvae in ballast water" (Aronson et al., 2007, p. 142). The presence of Subarctic *H. araneus*, a species already adapted to cold waters is a warning about the risks facing the Antarctic benthos in a time of increased human activity in Antarctic waters (Aronson et al., 2007, Tavares & De Melo, 2004). Numerous species of *Lithodidae* have been found to have extended their range into Antarctic waters with 14 species now known from the Southern Ocean (Aronson et al., 2007, Smith et al., 2012). *Neolithodes brodiei* in 2004 was discovered in waters off the Balleny Islands and was previously known from waters around New Zealand, representing the first record of a lithodid crab species extending its geographic range into Antarctic waters (Thatje & Lörz, 2005). In 2010, a significant reproductive population of *Neolithodes yaldwyni* was found in abundance over large areas of Palmer Deep on the WAP shelf providing evidence that "king crabs have crossed the Antarctic shelf" (Smith et al., 2012, p. 1017). In 2004, a further new record was found for the lithodid species *Paralomis birsteini*, represented by a

single individual crab found in the Bellinghausen Sea (Raso, Manjón, Ramos & Olaso, 2005). However, in 2010 off Marguerite Bay WAP, a reproducing population of *P. birsteini* was discovered living on Antarctic continental shelf (Aronson et al., 2015b). Furthermore, parallels can be drawn to the northern lithodid; *Lithodes maja* which has recently been recorded for the first time off the coast of Greenland (Aronson et al., 2007).

The new records of lithodid crabs in the Antarctic may represent recent invasions, and/or reflect the limited knowledge of distribution patterns of Antarctic species (Aronson et al., 2007, Griffiths et al., 2013, Raso et al., 2005). Furthermore, Griffiths et al. (2013) go on to argue that the presence of lithodid crabs in Palmer Deep and on Antarctic slope does not necessarily provide evidence to suggest that the populations will go on to move up onto the shelf itself. In response however, Aronson et al. (2015b) address this concern by evidencing the reproductive population of *P. birsteini* on Antarctic continental slope by showing that “there are no apparent physical or ecological barriers to impede the population from immediately expanding upward onto... the adjacent shelf, with potentially catastrophic impacts on the existing benthic fauna” (Aronson et al., 2015b p. 12998).

### **Ecological Impacts & Predation Pressure**

The presence of new durophagous predators will likely have significant impacts on the Antarctic shelf benthos, altering their structure and diversity and ultimately homogenising the ecosystems (Smith et al., 2012, Thatje et al., 2005b). The population density of *N. yaldwyni* at Palmer Deep is reported to be greater than that of the commercial fishery of *Paralithodes camtschaticus* in Alaska and similar in size to the “abundance of the lithodid *Paralomis formosa* being considered for commercial exploitation... on the South Georgia slope” (Smith et al., 2012, p. 1023); providing an indication of the significance of the invasion and potential current and future ecological impacts. Invasive lithodid crabs in the Arctic play a significant predatory role in Arctic food webs suggesting that Antarctic invasive lithodids could have equally severe predatory impacts on benthic ecosystems (Aronson et al., 2015a). Echinoderms and mollusks are common prey items for lithodid species therefore there is “no reason to expect that the population of *P. birsteini* would be food-limited were it to expand to the outer shelf” (Aronson et al., 2015b, p. 13000). The diversity of benthic communities was reported to be significantly lower at depths where lithodids were present than in areas where lithodids were lacking (Smith et al., 2012, Aronson et al., 2015b), with similar associated reductions in benthic diversity due to king crab invasions reported in the high Arctic

(Smith et al., 2012). The lack of echinoderms in particular, can be seen as indicative of crab presence in benthic communities on and up the Antarctic slope (Smith et al., 2012).

The reproductive viability of the king crab populations on the WAP shelf is widely discussed with a consensus that the populations are self-contained and reproducing (Aronson et al., 2015, Smith et al., 2012, Thatje et al., 2015). Smith et al. (2012) argue that 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” (Smith et al., 2012, p. 1024). Moreover, there appears to be limited predation pressure on lithodid populations establishing on the WAP (Aronson et al., 2015b). During the survey of the Marguerite Bay trench in 2010, predation pressure was estimated by reporting on the ‘sub-lethal damage’ of the limbs on the crabs photographed, concluding that limb injuries were rare in *P. birsteinii* with 1.2% of limbs damaged compared with temperate decapods exhibiting 22.8% damaged (Aronson et al. 2015b).

## Conclusion

The vulnerability of polar benthic ecosystems to invasion from species extending their range due to the anthropogenic climate change is widely accepted, and is likely to increase and become exacerbated in the coming decades as mean sea level temperatures increase (Thatje et al., 2005a, Smith et al., 2012). Whilst there is disagreement amongst scientists about elements of the lithodid invasion in the Antarctic, in particularly the Western Antarctic Peninsula, there is wide agreement regarding the imminent threat to the benthic fauna on the Antarctic shelf. An invasion of King Crabs, representing a ‘new’ top predator, to an ecosystem which has for millennia survived in the absence of durophagous predation, and evolved accordingly, will threaten many species and result in homogenisation of the ecosystem (Aronson et al., 2007). The way in which these ecosystems are managed and to what extent further human influence would help/hinder them is unclear. Warming will likely allow the entry of previously temperature-limited taxa onto the Antarctic shelf (Smith et al., 2012) with significant consequences for the indigenous benthic communities contributing to the diminished global diversity of marine ecosystems (Aronson et al., 2015b).

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