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Evolutionary drivers of biological adaptations to polar and deep seas

by

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Synopsis of achievements

Evolutionary drivers of biological adaptations to polar and deep seas

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1) Scale-dependent climatic drivers of Southern Ocean biodiversity

My research has led to a greatly improved understanding of the evolution of diversity of marine benthic organisms in the Southern Ocean and in response to climate oscillation over Milankovitch cycle of the late-Cenozoic, as well as the response of Antarctic marine invertebrates to current global warming [1-7]. This research has been of paradigm-changing nature, and by improving our understanding of how environmental constraints on organisms' life histories affect the resilience of species through time [1-4,8,9]. I have discovered and studied macrobenthic communities around Antarctica, including high latitudes of the sub-Antarctic, ranging from chemosynthetic environments such as whale fall and hydrothermal vent to extensive benthic communities of the Southern Ocean deep sea and continental shelves [10-16], including aspects of geographical and temporal changes [13-15,17,18]. My work contributed to the large-scale descriptions and understanding of unique community structures of the Antarctic benthos and expanded on the knowledge of these communities with respect to geographic range, production and productivity, and organismal diversity, with particular emphasis on peracarid and decapod crustaceans [7,13-15,17]. Further, my inventory of Southern Ocean benthic invertebrates [19,20] revealed that decapod crustaceans [20-22] and in particular reptant decapods are much more diverse, common, and widespread than previously described [20,23]. Within the reptant decapods, I have demonstrated that the globally diverse family of predatory lithodid crabs [20,23-25] is now established as diverse and widespread over large geographic areas off the continental shelves of Antarctica [7,23,25-27].

I utilise the early ontogeny of invertebrates as a model to assessing macro-ecological drivers (across physico-chemical and biological gradients), within past, present, and future climate scenarios [2,4,28]. This approach has allowed me to understand better the conditions whereby marine life endured the most severe environmental conditions prevailing during glacial periods and how life history constraints, such as on reproductive investment and dispersal stages [2,4], have affected the evolution of diversity of benthic organisms in response to climate oscillation over Milankovitch timescale covering the late Cenozoic [2-4,8,9]. My interdisciplinary research has also revealed that the conditions found at the Last Glacial Maximum have been by far more severe for polar life than previously believed [2,3], undoubtedly driving large scale oceanographic shifts in areas of Southern Ocean primary productivity and an associated latitudinal shift of marine life (or local concentration in open ocean polynya) during those periods [2-4]. I revealed that coastal polynyas characteristic of today's Southern Ocean did not exist during the Last Glacial Maximum. Consequently, much of the marine vertebrate, as well as invertebrate fauna, must have migrated to the ice edge and advection zone of the Southern Ocean's multiannual sea ice cover that covered most of the Southern Ocean in to today's sub-Antarctic latitudes [3,29]. Furthermore, the Antarctic continental shelf and slope were unfavourable environments for benthic communities during glacial periods, because of a variety of geophysical processes surrounding mass wasting and turbidity flows disturbing the seafloor beyond the edge of the grounding line of the continental ice sheets, which, in addition, expanded to the outer continental shelf at glacial maxima of the late-Cenozoic [2]. My research has shown that benthic community survival was only possible in the adjacent deep sea or in ice-free shelters on the continental shelf, which may have occurred as the result of the diachronism in maximum ice extent [2,4,8,9]. Indeed, population genetic study indicates a bottleneck event in the diversity of shallow water caridean shrimp populations associated with the last glacial maximum, leading to habitat contraction and explaining a reduced diversity of populations in those times [8]; species distribution models do also show that even deep-sea taxa have been affected by the multiannual sea-ice cover embracing the entire of the Southern Ocean; the multi-annual sea-ice cover which led to a complete shut-down of primary production and thus food availability, most likely driving many taxa to the advection zone associated with the ice edge [9].

Driven by climate oscillations of the Milankovitch cycle, the ability of marine invertebrates to withstand these fluctuations must have been much reliant on their capability for dispersal, for example in order to migrate between glacial shelters on the continental shelf, which

in turn must have affected the diversity of Antarctic benthos as we know it today [2,4]. Differences in early life-history patterns appear to be key to the resilience potential of species in response to shelf ice fluctuations across the continental shelves in glacial periods, and there appears to be a direct relationship between the rate of speciation and the ability of taxa to disperse [2,4].

Compared to elsewhere in the sea, Southern Ocean invertebrates show a high level of brooding species across many phyla [30-34], however, broadcasting species also exist and tend to dominate reproductive traits of marine invertebrates at Sub-Antarctic latitudes [35-40]. Cold polar temperatures, as well as strong seasonality in food availability, have driven the evolution of ecophysiological adaptations in brooding species peculiar of this environment [4,31,32,41,42]. Low fecundity, seasonal or aseasonal reproduction, large offspring and slow growth do generally characterise these species [31-34]. Evolutionary temperature adaptation is also seen in broadcasting taxa with planktotrophic or planktonic/demersal and lecithotrophic developments. Indeed, temperature is the main driver of per offspring investment (POI) and my research has shown that temperature shifts, as found along latitudinal clines and with depth, drive the allocation of higher POI with decreasing temperature [43-47]. Such clines in reproductive traits are even evident within subtle latitudinal temperature changes of the Southern Ocean [48], and some decapod crustaceans in these waters show a POI that allows for exceptionally long lecithotrophy in larvae and juveniles sometimes exceeding a year in duration [49,50]. An increase in POI in decapod crustaceans goes hand in hand with an abbreviation of the life cycle, with fewer but morphologically more advanced larval stages [35,36,38,39,50-52]. Taken together, evolutionary temperature adaptation provides important insight in the evolution of endotrophy and fully food independent larval development [53,54]. This is also evidenced by phylogenetically supported studies of POI in lithodid crabs at global scale, where temperature is the significant driver of POI [47,49].

Lessons learned from my research on the resilience potential of life in cold-stenothermal environments also contribute significantly to our ability to predict the future of polar invertebrates to rapid climate change, in particular along the Western Antarctic Peninsula [1,2,5-7,55]. My research was first to highlight the potential for species intrusions in to the Southern Ocean from adjacent sub-Antarctic waters [5,6,55]. My research was also first to demonstrate that, as a result of surface water warming in response to climate warming along the Western Antarctic Peninsula, deep-sea species of the continental slope are capable of emerging into shallow continental shelf waters [1,7]. This research demonstrated that the emergence of

predatory lithodid (king) crab into these continental shelf waters will be of catastrophic effect for the paleozoic-type shelf fauna that evolved in the absence of major benthic predators since at least the end of Antarctic cooling some 16 Ma ago [1,7,27,56]. The introduction of seafloor predators such as decapod crabs into the warming seas of Antarctica, either through latitudinal or bathymetric range extensions or by anthropogenic means of transport such as ballast water transport will significantly restructure seafloor communities and be of detriment to these species, in addition to the already detrimental effects of global warming [1,5-7,27,28,55]. I have shown that the biogeography of Southern Ocean invertebrates is driven by subtle differences in temperature within the cold-stenothermal environment [57]. In this context, the long-term effects of warming on the ecology of a marine bivalve over a 40-year period have been described [58], highlighting that Antarctic marine invertebrates possess slightly variable levels of resilience to thermal stress among species and populations and within their cold-stenothermal adaptation [59]. Despite these subtle differences in thermal resilience however, climate warming remains a challenge to all of them.

2) The role of hydrostatic pressure in governing aquatic biodiversity

Over the course of the past decade, I have revolutionised our understanding of how marine organisms thrive under hyperbaric conditions. I have established scientific methodologies [60-66] and analytical protocols [66-70] to assess experimentally the ecological and physiological responses of marine invertebrates to environmental stressors namely temperature and hydrostatic pressure [64,71,72]. Within a few years of this research, and resulting from experimental work carried out both on land and at sea, I developed an understanding of how the deep ocean may have been colonized by shallow-water organisms, in particular following large-scale extinction events of the geological past [73]. My research challenges previous ideas of an evolutionarily slow process in the transition of life from shallow to deep seas; indeed, this research suggests that migration of species to greater depths may be rapid (perhaps a matter of generations) and in response to the intensity of natural/anthropogenic perturbations. This research corroborates suggested process of past shifts in depth range in response to climatic drivers [2,8,73], including the emergence of deep-sea organisms into shallow-water, which at high latitudes of polar seas is facilitated by polar isothermy [2,7,8]. My research also provides a novel mechanistic insight into the physiological processes of temperature–pressure acclimation and tolerance [71,72,74]. Further, it also provides an evolutionary perspective for shifts in depth range in ectotherms away from isothermal water bodies, particularly at temperate latitudes. Such knowledge is key to

understanding better physiological bottlenecks in the radiation and speciation of organisms throughout the oceans [7,8,73,75].

The physiological and combined hydrostatic pressure and temperature window that is tolerated by marine ectotherms depends on a species' ancestral experience over its evolutionary past. To identify the different thermal pathways in evolutionary pressure and temperature adaptations, my research has focused on key species with well-established phylogenies that allow for identifying past climate bottlenecks in their radiation history [67,68,75,76]. Whether a species is of cold- or warm-water origin has been shown to play a fundamental role in the ability of extant species to tolerating pressure [60,66-68,75,77]. Striking similarities in physiological responses have been found in deep-sea and related shallow-water faunas at various levels of organismal organisation, ranging from respiratory physiology, thermal tolerance to heat-shock protein responses, pointing at close evolutionary histories [60,67,68,78]. Cold-water adaptation has been found in species of cold-water origin, the common whelk *Buccinum undatum*, in which a combination of low temperatures and high hydrostatic pressures demonstrates the greatest physiological tolerance [77,79]. Unique in this research was the establishment of full thermal and pressure tolerance windows in several species under investigation [62,71,78-80]. A remarkable feature is that all species under investigation, whether of cold or warm water origin, were shown to tolerate pressures much greater than those found over their natural bathymetric range [62,71,73,77,80]. This physiological scope is key to the hypothesis that many marine ectotherms are readily adapted, at least in terms of physiological scope, to change their depth distribution in response to ecosystem perturbations.

Hydrostatic pressure tolerance can be assessed at various levels of organisation of an organism. I have demonstrated that the hydrostatic pressure scope of an organism is narrowed by specific dynamic action (SDA), such as feeding or escape response [64,65]. This is crucial, as ectotherms do present much greater pressure and thermal tolerances in a standard (resting) metabolic rate [62,64] when excluding any SDA, which is key to the animals' ecology and therefore long-term sustenance. Maximum heart rate is a good indicator of approaching a hyperbaric threshold, alongside reaching a maximum in respiration rate or a collapse of the same [61,65,66]. Standard (resting) metabolic rate is generally affected by temperature, whereas behaviour responds much earlier to an increase in pressure [64]. Loss of equilibrium – when an organism falls on its side – is also a good indicator of pressure tolerance as well as preceding limits in respiratory capacity [62,71,72].

To assess the stress response to pressure and temperature at cellular level, I used stress-70 proteins [67-70,81] as well as genetic markers for the respiratory and neurological systems [70,82]. It has been shown that related deep-sea and shallow-water shrimp respond to temperature stress at different levels of magnitude with regard to heat-shock protein (HSP70) response, indicating a high level of plasticity in response to thermal stress [67,68,83]. In shallow-water species acclimated to different temperatures, the thermal resilience improves with acclimation history, and a heat-shock response can still be elicited at temperatures above those experienced in nature [84]. By exploring the molecular basis of pressure tolerance I was able to show that the shrimp *Palaemon varians* shows significant increases in the transcription of genes coding for a *N*-methyl-D-aspartate (NMDA) receptor-regulated protein, an ADP ribosylation factor, β -actin, two heat shock protein 70kDa isoforms (HSP70), and glyceraldehyde-3-phosphate dehydrogenase (GAPDH) in response to elevated pressure [69,70]. These data indicate that the sub-lethal effects of barotrauma are associated with transcriptional disturbances within the nervous tissue of crustaceans, and cellular macromolecular damage [69,70,82]. Such transcriptional changes lead to the onset of symptoms similar to that described as High Pressure Neurological Syndrome in mammals, and may act as a limit to shallow water organisms' prolonged survival at depth [70]. I demonstrated a decrease in hydrostatic pressure tolerance as ontogeny advances, as demonstrated in the larval development of lithodid crab [85], which is critical when assessing the ability of marine invertebrates to disperse.

By establishing a synthesis describing physiological mechanism, I could show that NMDA receptor regulation underlies physiological intolerance to both low temperature and high hydrostatic pressure [74], where pressure can diminish the efficacy of receptor blockade and augment NMDA receptor synaptic responses, leading to hyper-excitability and potentially to neurotoxicity. Where naturally occurring or anthropogenically-mediated metal toxicants, such as copper and cadmium, come into play, low temperature has been shown to reduce toxicity (survival rates) in both metals [86,87]. By contrast, elevated pressure increased copper toxicity but did not affect cadmium toxicity [87]. These findings are important when assessing species' resilience to environmental effects on toxicity [88].

I demonstrated that the depth distribution of marine ectotherms is predominantly limited by their ability to maintain aerobic metabolism [64-66,89]. Though the hypoxia threshold appears to determine depth tolerance, hydrostatic pressure does still play an important role in this process [63,89]. When depth is included in a conceptual model of determining the Fundamental Ecological Niches (FEN) of marine invertebrates and fishes, it has been demonstrated for the

first time that temperate as well as tropical faunas experience FEN expansion – with regard to depth – with ocean warming, although polar fauna experience the greatest FEN contraction. The ability of marine ectotherms to respond to ocean warming by e.g. moving to greater water depths is of increasing concern. In this context, I showed that, indeed, at least some marine caridean shrimps, e.g. of the genus *Palaemon*, are capable of rapidly making use of their physiological scope and quickly complete acclimation – within only a week – to deep-sea conditions [71,72]. The model genus *Palaemon*, which is related to hydrothermal vent bresiliid shrimp, provides important insights into the evolutionary pathways of colonising the deep sea. The capacity to tolerate deep-sea pressures in this context has also been shown for mollusc species [60,77,80] and other decapod crustacean [66].

Both temperature and hydrostatic pressure have been shown to govern the evolutionary history of marine ectotherms by providing bottlenecks, as well as physiological avenues, to their radiation and speciation over geological periods of time [8,75,76]. In this context, I demonstrated that the step from shallow to deep living is of energetic cost to the organism. Indeed, reproductive expenditures in embryo development have been shown to increase under hydrostatic pressure, and this increased metabolic cost seen in shallow-water organism exposed to deep-sea pressures does indicate the need for metabolic adaptation in the transition to deep-sea life [90], at least when transitioning to abyssal depths. It should be noted however, that it is temperature not pressure that has been shown to be significant as a selective force behind an increase in per offspring investment (POI) in lithodid crabs [47,49]; POI does increase with ocean depth and within a framework supported by the phylogenetic history of decapod crustacean family (Lithodidae) [75,76].

The hyperbaric physiology research carried out to date already points at a phenomenon of global scale that has been widely ignored: the potential necessity for organisms to respond to surface water warming or other forms of natural or anthropogenic ecosystem disturbance by moving to greater depth. Potential habitat contractions across depths in response to environmental drivers, such as surface water warming or ocean acidification, have previously been recognized. The assessment of the ability of organisms to respond to these has been championed by my research. I advocate that understanding the ‘winners and losers’ of tomorrows’ race for habitat at greater depth [72,73,77,89], will be of equal importance to the once groundbreaking and long established understanding of latitudinal shifts in the distribution of organisms in response to global warming.

Selected publications on which DSc submission is based

[publications listed in order of appearance in DSc Synopsis]

(statement indicating nature and contribution to each publication by applicant)

(*) reference to ten most significant publications

1) *Scale-dependent climatic drivers of Southern Ocean biodiversity*

[1] (*) **Thatje, S.**, K. Anger, J.A. Calcagno, G.A. Lovrich, H.O. Pörtner, W.E. Arntz (2005). Challenging the cold: crabs reconquer the Antarctic. *Ecology*, 86 (3): 619-625.

(ST conceived idea, analysed data, and wrote article).

[2] (*) **Thatje, S.**, C.D. Hillenbrand, R. Larter (2005). On the origin of Antarctic marine benthic community structure. *Trends in Ecology & Evolution*, 20 (10): 534-540.

(ST conceived idea, wrote article in collaboration with co-authors).

[3] (*) **Thatje, S.**, C.D. Hillenbrand, A. Mackensen, R. Larter (2008). Life hung by a thread: endurance of Antarctic fauna in glacial periods. *Ecology*, 89(3): 682-692.

(ST conceived idea, wrote article in collaboration with co-authors).

[4] **Thatje, S.** (2012). Effects of capability for dispersal on the evolution of diversity in Antarctic benthos. *Integrative and Comparative Biology*. 52 (4): 470-482. DOI: 10.1093/icb/ics105

(ST conceived idea and wrote article).

[5] (*) Aronson, R.B., **S. Thatje**, A. Clarke, L.S. Peck, D.B. Blake, C.D. Wilga, B.A. Seibel (2007). Climate change and invasibility of the Antarctic benthos. *Annual Review of Ecology, Evolution, and Systematics*, 38: 129-154. DOI:10.1146/annurev.ecolsys.38.091206.095525

(ARB and ST conceived the study and wrote article in collaboration with co-authors).

[6] Aronson, R.B., **S. Thatje**, J.B. McClintock, K.A. Hughes (2011). Anthropogenic Impacts on Marine Ecosystems in Antarctica. Book Series: Year in Evolutionary Biology. *Annals of the New York Academy of Sciences* 1223: 82–107. DOI: 10.1111/j.1749-6632.2010.05926.x

(ARB and ST conceived the study and wrote article in collaboration with co-authors).

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- (2015). No barrier to shoreward expansion of bathyal king crabs on the Antarctic Shelf. *Proceedings of the National Academy of Sciences*. doi:10.1073/pnas.1513962112
(ST conceived idea, which was then developed further with ARB; ST contributed to data analysis, and co-wrote article).
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(ST and MJP conceived idea; ST co-wrote article).
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(PhD work JD; ST developed idea with JD and MJR, and co-wrote article).
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(ST contributed to idea, data, and co-wrote article).
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(WEA, KL and ST developed idea, carried out data sampling and analyses, ST co-wrote article).
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(ST participated in fieldwork; contributed to analyses, co-wrote article).
- [13] Rehm, P., **S. Thatje**, W.E. Arntz, A. Brandt, O. Heilmayer (2006). Distribution and composition of macrozoobenthic communities along a Victoria-Land transect (Ross Sea, Antarctica). *Polar Biology*, 29: 782-790. doi:10.1007/s00300-006-0155-8

(PhD work PR; idea developed by all; ST contributed to data analysis, and co-wrote article).

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(PhD work PR; ST, AB and PR developed idea; ST co-wrote article).

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(ST co-wrote manuscript and developed idea and data analysis with KES).

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(ST analysed data and wrote article).
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(ST co-wrote article).

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(ST conceived idea; contributed to data, co-wrote article).

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Research Statement

I am a marine ecologist studying the evolutionary history of life in the sea, with special focus on the ecological and physiological adaptations of invertebrates to extreme ambient conditions prevailing in polar and deep-sea environments. I prioritize a highly multidisciplinary approach to my research, and aspire to unify the natural sciences, ranging from physiology, molecular biology, paleoecology, geology and geophysics within the encompassing field of ecology. I remain particularly interested in macroecological concepts, such as temperature-driven traits in reproduction as a result of latitudinal shifts in temperature and food availability. As part of such studies, I strive to understand better how the environment fosters maternal offspring provisioning and larval developmental plasticity, explaining traits found at intra- and inter-specific levels. Such knowledge is key to understand the mechanisms behind macroecological patterns of reproduction and diversity, observed with both depth and latitude. Furthermore, such knowledge allows predictions to be made for the future of marine biodiversity and biogeography in a rapidly changing world.

Professional career

October 2014 – to date	Associate Professor in <i>Marine Evolutionary Ecology</i> .
March 2011 – Sept 2014	Senior Lecturer in <i>Marine Evolutionary Ecology</i> .
August 2005 – March 2011	Lecturer, National Oceanography Centre, Southampton, School of Ocean and Earth Science, University of Southampton, United Kingdom.
Oct 2004 – Sept 2008	Coordinator of a project within the 6. European Framework Programme (INCO-STREP, “Climate variability and El Niño Southern Oscillation: implications for coastal natural Resources and management, CENSOR ”, total budget 3 Million EURO).
May 2003 – July 2005	Post-Doctoral Researcher at Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, Departments: Comparative Ecosystem Research & Ecophysiology & Ecotoxicology; in collaboration with British Antarctic Survey, Cambridge, UK
Jan 2001 – May 2003	PhD-student, University of Bremen and Alfred Wegener Institute for Polar and Marine Research, Bremerhaven. PhD thesis: “Reproductive trade-offs in benthic decapod crustaceans of high southern latitudes: tolerance of cold and food limitation”, Disputation (Dr.rer.nat.): June 10, academic result “ <i>summa cum laude</i> ” (highest possible award).
March 2000	‘Dipl. Biol.’ (Master Sci.), University of Kiel, title of thesis: “Distribution and development of benthic macrofauna communities of the inner German Bight”.
1995 – 2000	Studies in Zoology, Marine Biology, Physical Oceanography, Marine Chemistry, University of Kiel, Germany.
1994 –1995	Social Service, Hospital Preetz.
June 1994	Matriculation, Internatsgymnasium Schloß Plön (Germany).

Citation Index

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Research Gate: RG Score **41.93** (accessed 08/08/19)

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