



OPINION PIECE

# Climate warming affects the depth distribution of marine ectotherms

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**ABSTRACT:** Climate change causes warming of the oceans, and there is consensus that many marine ectotherms, including marine invertebrates and fishes, respond to the increase in temperature by showing latitudinal range shifts in their distribution. However, the effect of ocean warming on the bathymetric distribution of marine ectotherms remains largely theoretical, and few works evidence bathymetric range shifts. Since warming is not exclusive of surface waters, the depth distribution of species should also be affected by warming. Here, I exemplify bathymetric distribution ranges of marine ectotherms from the North Atlantic and advocate that there will be species-specific shifts in the fundamental ecological niches occupied in response to climate warming. Combined temperature and pressure acclimation to match oxygen capacity demands at physiological thresholds is key to this process. Species-specific tolerance of hydrostatic pressure and temperature determines depth distribution ranges of marine ectotherms.

**KEY WORDS:** Climate change · Biogeography · Bathymetric distribution · Latitude · Temperature · Hydrostatic pressure

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## 1. INTRODUCTION

Latitudinal shifts in the distributions of marine ectotherms in response to climate warming are well known, yet the potential for shifts in the depth distributions of marine ectotherms in response to warming remains largely unexplored. Shifts in depth range have been generally overlooked when exploring the significance of geographic range shifts to global warming (Pinsky et al. 2013, Deutsch et al. 2015). It has been demonstrated that in some species, the deepening rate in response to warming can be comparable to latitudinal shifts (e.g. fish assemblage deepened by  $\sim 3.6$  m decade<sup>-1</sup>) (Dulvy et al. 2008, Pinsky et al. 2013). Warming is not restricted to surface waters (Balmaseda et al. 2013), and therefore, any marine ectotherm thriving at greater ocean depth will be affected by a warming environment

(Perry et al. 2005, Weinberg 2005, Somero 2012, Beaugrand et al. 2014).

It has been shown that marine ectotherms have responded to environmental change, including climate change, in the geological past. Furthermore, transitions from shallow to deep-water depths have been identified in the radiation histories of species (Brown & Thatje 2014, Hall & Thatje 2018). Indeed, onshore–offshore patterns of evolution in the radiation and speciation of species following mass-extinction events in the deep sea (>200 m) in response to e.g. large-scale dysoxic conditions, is supported by the fossil record (Jablonski et al. 1983). The exact drivers of such processes leading to colonisation of deeper waters by shallow-water organisms have not yet been identified, but climate change likely plays a significant role (Brown & Thatje 2014).

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Current conditions of rapidly warming seas present an unprecedented case from which we can learn about the pace at which geographic range shifts can take place. Average sea surface temperature is predicted to increase, reaching between 1 and 3°C higher in the period 2081–2100 than in the period 1986–2005 (Collins et al. 2013), accompanied by significantly greater thermal variability (Lima & Wethey 2012). Previous research also predicts that climate warming will see habitat contraction across ocean depths (Levin & Sibuet 2012). Because of low temperature adaptation and poleward constraints on biogeographic ranges, polar marine taxa are predicted to be challenged the most (Parmesan & Yohe 2003, Brown & Thatje 2015, IPCC 2019). Furthermore, temperature in deeper waters is estimated to warm more slowly than sea surface temperatures (Balmaseda et al. 2013). Nevertheless, the whole ocean will eventually and gradually warm up over the next approximately 500–1000 yr (Li et al. 2013), exposing taxa from deeper waters typically adapted to cold-stenothermal conditions to thermal stress (Brown & Thatje 2014). Acclimation to lower temperatures and high hydrostatic pressure (HP) requires integrated homeoviscous modifications in the saturation of membrane lipids (Pörtner 2002), alongside unsaturation of fatty acids in order to maintain membrane function at lower temperature and/or high HP. Changes in phospholipid fatty acid composition hint at cellular responses against low temperature- and/or HP-mediated decrease in the permeability and fluidity of membranes (Somero 1992, Hazel 1995).

I advocate a working hypothesis that marine ectotherms will respond to surface water warming by submerging into deeper, cooler regimes, which is so far only supported by few available studies (Perry et al. 2005, Weinberg 2005, Dulvy et al. 2008, Pinsky et al. 2013, Burrows et al. 2019). Recognising this process is as significant as the established concept of latitudinal range shifts in species in response to global warming. I predict that acclimation to temperature and HP is key to match oxygen capacity demands at physiological thresholds, enabling a shift in bathymetric distribution.

## 2. PHYSIOLOGICAL LIMITS TO DEPTH DISTRIBUTION

A physiological bottleneck limiting depth range extension in species from shallow waters is likely being defined by the effects of HP. Nevertheless,

bathymetric range limitation by threshold levels of HP has rarely been demonstrated, and thus the potential mechanism constraining hyperbaric tolerance remains largely theoretical.

Here, I hypothesise that the physiological and combined HP and temperature window that is tolerated by marine ectotherms depends on the ancestral experience of a species over its evolutionary past. To identify the different thermal pathways in evolutionary HP and temperature adaptations, my research has previously focussed on key species with well-established phylogenies that allow for identifying past climate bottlenecks in their radiation history (Hall & Thatje 2009, 2018, Cottin et al. 2010, 2012). Whether a species is of cold- or warm-water (phylogenetic) origin has been shown to play a fundamental role in the ability of extant species to tolerate pressure (Mestre et al. 2009, Smith et al. 2013, Brown et al. 2017). For example, species with phylogenetic origin in temperate seas tolerate a combination of warm-eurythermal waters and high HP much better than species with a cold-water phylogenetic origin that tolerate high HP better in a cold-water, isothermal setting (Mestre et al. 2009, Smith et al. 2013, Brown et al. 2017).

I have demonstrated that the depth distribution of marine ectotherms (Fig. 1) is predominantly limited by their ability to maintain aerobic metabolism. This has been studied by e.g. assessing how specific dynamic action such as feeding or escape response cause a mismatch between oxygen supply and demand by the organism (Thatje et al. 2010, Thatje & Robinson 2011, Brown et al. 2017). Although the hypoxia threshold appears to determine depth tolerance, HP still plays an important role in this process (Brown & Thatje 2011, 2015). When depth is included in a theoretical model of determining the fundamental ecological niche (FEN) of marine invertebrates and fishes, which in the present context refers to the 3-dimensional habitat occupied, it has been demonstrated that faunas from temperate and tropical regions experience FEN expansion — with regard to water depth — with ocean warming, whereas polar fauna experience the greatest FEN contraction (Brown & Thatje 2015, Burrows et al. 2019). This model is based on the assumption that physiological limits to HP tolerance are defined by oxygen limitation to the organism (Brown & Thatje 2015).

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 it has been shown that at least some marine caridean shrimps, e.g. of the genus *Palaemon*, which are re-

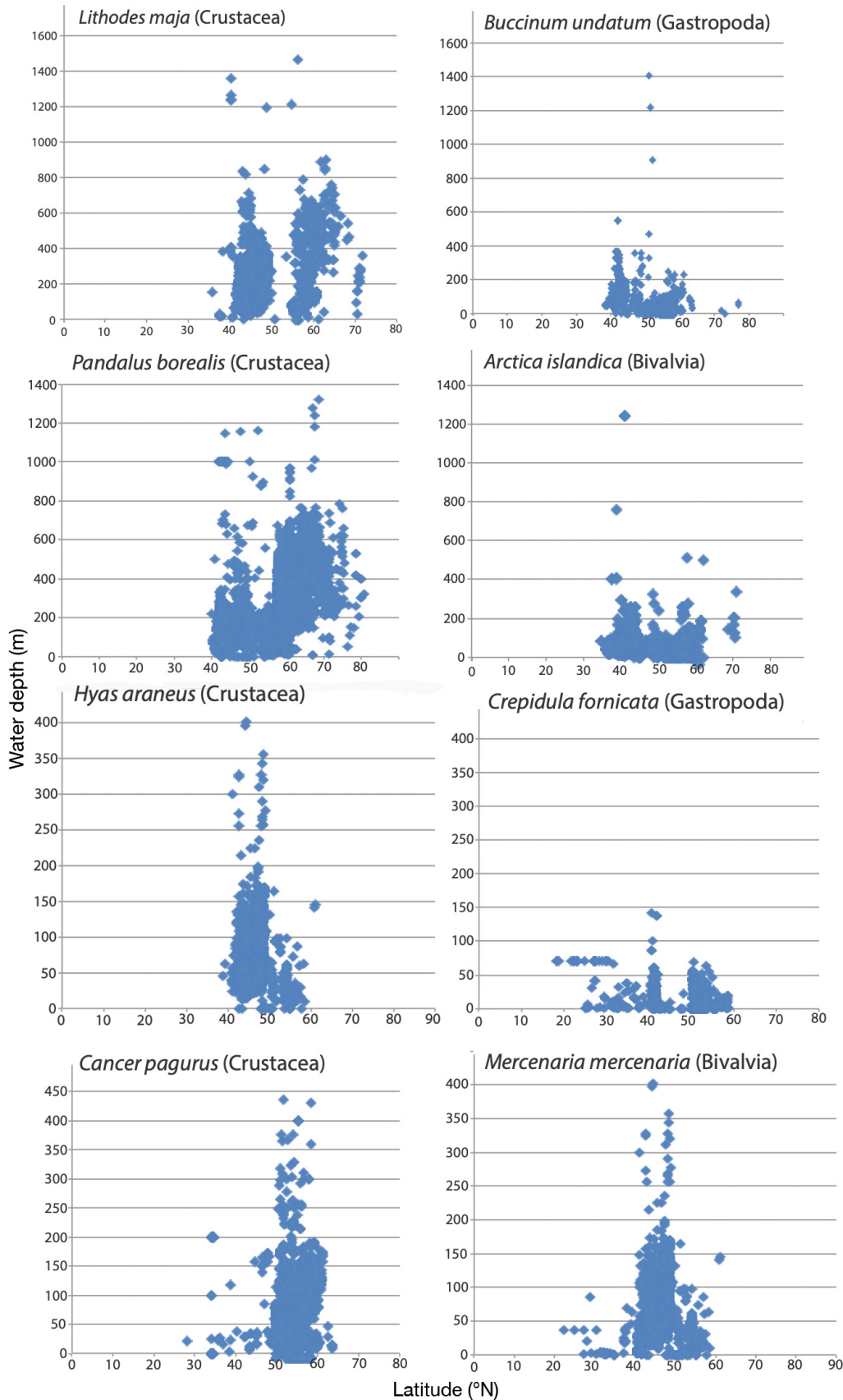


Fig. 1. Latitudinal and bathymetric distribution of select marine ectotherms from the North Atlantic. Data are from OBIS (2020) and represent single records. Distribution patterns are species-specific but show a degree of niche overlap. Distribution ranges are approximations based on available data, and it must be considered that many deep-sea areas are presently under-sampled. Thus, true distribution ranges may be underestimated

lated to deep-sea bresilid shrimp, are capable of rapidly making use of their physiological scope and quickly complete acclimation, within only 1 wk, to deep-sea conditions (New et al. 2014). Indeed, and when conceptualising the available knowledge, it emerges that acclimation leads to a capacity (scope) increase (Ravaux et al. 2012) in the critical thermal and critical pressure tolerance of ectotherms (Fig. 2), where species of warm-water (phylogenetic) origin show a major increase in HP tolerance, and species of cold-water (phylogenetic) origin show a moderate increase (tested in mollusc and decapod species; Mestre et al. 2009, Smith et al. 2013, Brown et al. 2017).

Species interactions and associated potential shifts in food webs, such as a depth-related response to warming, is species-specific. Further, climate warming causes selection for greater acclimation capacity and, therefore, will enable a capacity increase in cold-stenothermal/eurythermal (sub-polar to polar) to warm-eurythermal (temperate) ectotherms (Fig. 2). It is likely that marine ectotherms will respond to habitat contraction across depth due to warming by migrating to greater ocean depths (Levin & Sibuet 2012). However, this process is not entirely of physiological nature, the same as is the extant bathymetric range of marine ectotherms (Fig. 1). It should not be overlooked that food conditions and the possible physiological constraint for light can also become limiting factors.

A precise analysis of the effects of a changing climate on the depth ranges of species is affected by uncertainty regarding the importance of HP in limiting bathymetric distributions, which generally receives little consideration, and the accessibility of environmental data (Brown & Thatje 2014, 2015, Deutsch et al. 2015). Physiological bottlenecks (e.g. oxygen limitation) governed by the effects of high HP and low temperature on deep continental margins drive biodiversity patterns of marine ectotherms which colonised the deep sea following mass extinctions in the geological past (Brown & Thatje 2014). Nevertheless, this concept remains largely theoretical, as there has been little demonstration of hyperbaric limits to bathymetric/depth ranges (Brown & Thatje 2014, 2015).

The concept of oxygen-limited thermal tolerance, whereby the capacity to supply enough oxygen to meet metabolic demand defines thermal tolerance (Pörtner 2010), also applies to hyperbaric limitation (Brown & Thatje 2014, 2015). Principles of energy allocation in dynamic energy budget models (Kooijman et al. 2008) have been integrated with this con-

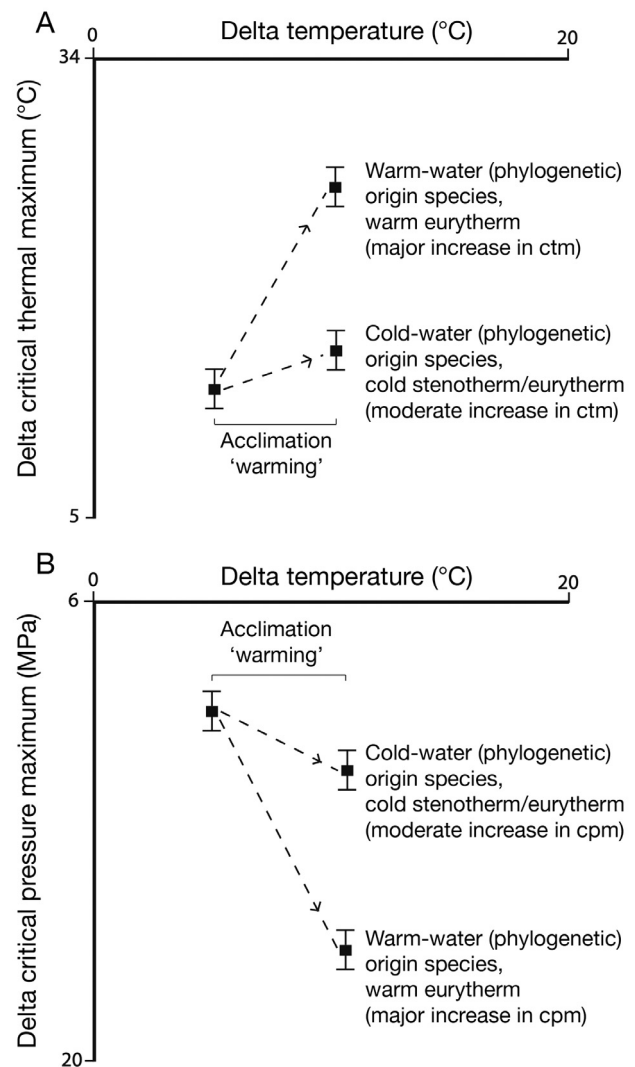


Fig. 2. Conceptualisation of the effect of climate warming (estimated 1–3°C until the year 2100, Collins et al. 2013) on the (A) critical thermal maximum (ctm) and (B) critical pressure maximum (cpm) in marine ectotherms from cold-stenothermal/eurythermal (polar to sub-polar) to warm-eurythermal (temperate) regions. Long-term acclimation ('warming') over multiple generations leads to a capacity increase by selection for thermal scope (Ravaux et al. 2012), which is greater in species of warm-water (phylogenetic) origin than in those of cold-water (phylogenetic) origin. Bathymetric range is expanding in either case. Acclimation is not possible where the thermal limit has been surpassed. The cold/warm-water (phylogenetic origin) scenarios given in both graphs are for distinct species and do not originate from the same species. Error bars represent standard deviation

cept to deliver a conceptual bioenergetic framework of stress tolerance (Sokolova 2013). This idea facilitates incorporation of the physiological effects of (environmental) stressors, relating these to long-term

consequences at the population level, and distinguishing moderate environmental stress in sustainable populations from high/extreme stress limiting species distributions (Sokolova 2013). Further, it points out the importance of experimentally checking the adequacy of the assumptions on which the established models are based. For example, the transition to sustained moderate hyperbaric stress in the lithodid crab *Lithodes maja* precedes the species' known distribution limit of 790 m and suggests that it is the metabolic cost related to hyperbaric stress that constrains depth distribution. This result suggests including HP in a framework of energy-constrained biogeographic range in aquatic ectotherms, which is affected by the costs that result from living under sub-optimal environmental conditions (Sokolova 2013).

### 3. BATHYMETRIC DISTRIBUTION OF NORTH ATLANTIC FAUNA

Marine ectotherms present species-specific latitudinal and bathymetric distribution patterns as represented by select species from the North Atlantic (Fig. 1). In order to demonstrate this, I have chosen cases with high sample size and spatial resolution (>8000 data points [OBIS 2020]; data have been cleaned), which may still underestimate true species distribution ranges. Some species describe a narrow (e.g. *Hyas araneus*) or wide (e.g. *Mercenaria mercenaria*) bell-shaped or bi-modal (e.g. *Lithodes maja*, *Pandalus borealis*) bathymetric distribution pattern across latitude (Fig. 1).

Although the presented taxa present niche overlap with regard to both latitudinal range and depth distribution, their distribution is also species-specific, with some being e.g. more eurybathic than others (Fig. 1). The distribution pattern for each species presents a high density of core data, which, given the high sample resolution, indicates optimal distribution ranges. This core distribution does not necessarily represent the centre of its latitudinal or depth range, and most likely represents ecophysiological optimal conditions at those locations. Towards both bathymetric as well as latitudinal distribution limits, sample records become scarcer and demonstrate a scattered pattern, representing few species records (e.g. *Arctica islandica*, Fig. 1).

In a theoretical framework, these areas identify zones where ecological and/or physiological conditions are sub-optimal for sustaining populations.

Limits in biogeographic range generally occur before transitioning to moderate/extreme stress (Pörtner & Farrell 2008, Sokolova 2013). Populations of many marine ectotherms from distributional margins thrive at environmental temperatures which correlate with critical temperatures that cause organisms to develop stress. Thermal thresholds are defined by the costs involved in the response to stress (Pörtner & Farrell 2008, Sokolova 2013), which are often mediated by physiological and/or behavioural mechanisms (Fehsenfeld & Weihrauch 2017), and this requires a flexible allocation of energy (Sokolova 2013). The distribution range either of latitudinal or bathymetric extent is the sum of a number of populations (e.g. genetic haplotypes) represented by each species. At the margin of distribution ranges, the presence of adult populations does not necessarily imply that the population is self-sustained. Less than typical abundances may be signs of increased ecological and physiological competition with species that adapt better to local e.g. thermal or food conditions. The species demonstrated are commonly known key species (Fig. 1).

In the North Atlantic, species with wide and narrow latitudinal ranges and either steno- (e.g. *Crepidula fornicata*) or eurybathic (e.g. *P. borealis*) distribution ranges coexist (Fig. 1). Interestingly, *P. borealis* avoids shelf sea depths at sub-Arctic to Arctic latitudes representing low, polar temperatures, and this process of polar submergence leads to greater depth penetration. The lithodid crab *L. maja* shows a similar tendency (Fig. 1).

### 4. DISTRIBUTION RANGE SHIFTS AND POPULATION-SPECIFIC RESPONSES

HP plays an important role in constraining the biogeographic range of marine ectotherms. It is generally known that ectotherms tolerate greater HP than that which corresponds to their natural bathymetric range and may therefore be seen as readily adapted to a changing environment (Brown & Thatje 2014). Species-specific tolerances of HP and temperature must be considered when assessing the effects of climatic change, such as warming or ocean acidification, on the bathymetric distribution of taxa (Brown & Thatje 2014, 2015, Morris et al. 2015). Environmental temperatures in populations from distributional limits of marine ectotherms often identify with critical temperatures at which species develop moderate/extreme stress. Thermal thresholds of species distributions therefore often seem determined by ener-

getic costs related to the thermal stress response (Pörtner & Farrell 2008, Sokolova 2013). When defining depth distribution limits of species, conditions of similar energetic cost must be assessed for combined tolerances of HP and temperature (Brown & Thatje 2015).

A theoretical approach for the first time demonstrated that when depth distribution is included in a conceptual model for determining the FEN of marine ectotherms, marine faunas experience shifts in FEN in response to climate warming, which is the cause of a shift in oxygen limitation with water depth. As previously highlighted, faunas from different climate zones either experience FEN expansion or contraction, but all of them show an increase in bathymetric distribution of marine ectotherms, which I suggest is a consequence of acclimation to both temperature and HP (Fig. 2) (New et al. 2014). Consequently, assessing the ability of species to escape surface warming by submerging to greater depth must be of scientific concern. Given the species-specific bathymetric distributions highlighted in this paper, a species-specific response to warming is also to be anticipated with regard to bathymetric range. There may even be population-specific responses in species with wide distribution range. A previous study showed that there are population-specific responses of heat-shock tolerance, which constitutes an acute thermal protective mechanism, in marine ectotherms (Ravaux et al. 2012). Selection induced by global warming will likely occur in each population. Similar evolutionary mechanisms are to be expected with regard to population-specific adaptations to the combined effect of changes in both HP and temperature. Latitudinal shifts in temperature are known to change ecological adaptations across populations, for example by shifting the timing and extension of reproductive periods, which can cause reproductive isolation between populations (Smith & Thatje 2012, Smith et al. 2013). There is also first evidence that shifts in temperature with ocean depth cause reproductive isolation of invertebrate populations over depth range (Gage & Tyler 1982). Such changes in life history are fundamental when assessing the resilience of populations to environmental changes, and such knowledge is crucial when predicting e.g. the viability and use of fisheries stocks under current and future climate warming scenarios.

Consequently, science needs to do more to assess changes in FEN, species–species interactions, and the effects of related phylogenies in response to environmental change. Based on the available environmental and distributional data, detailed modelling of

FENs (or the realised niches) of species may now be possible, at least for select taxa (Burrows et al. 2019). Ecophysiology needs to look into population-specific traits with regard to both latitudinal and bathymetric distributions of taxa, and molecular biology needs to look into population connectivity (e.g. haplotype diversity networks) across bathymetric distributions to assess the identity, relatedness and origins of populations. This may help to assess past as well as predict future winners and losers of climate warming.

## 5. CONCLUSIONS

I hypothesise that many marine ectotherms respond to surface water warming by moving to greater water depths, and that this response will be species-specific and will depend on their evolutionary origin, as well as on biotic factors (e.g. food resources, ecological competition, niche availability). Potential habitat contractions across depths in response to environmental drivers, such as surface water warming or ocean acidification, have previously been suggested (Levin & Sibuet 2012); however, limited data, including a lack of available 3-D environmental data, assessing depth-related biogeographic range shifts exist to support this. We need to study how the phylogenies (evolutionary histories) of marine ectotherms affect species' scopes in tolerating both temperature and HP in a warming climate. How do species-specific responses in temperature and HP tolerance affect shifts in benthic assemblages and associated food webs, and how may such shifts affect the overall carbon flux in the ocean? These questions are paramount when assessing vertical transitions of ecosystem change in response to warming. Finally, I advocate that understanding the 'winners and losers' of tomorrow's race for habitat at greater depth will be of equal importance to the long-established concept of latitudinal shifts in the distribution of species in response to climate warming.

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