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CLIMATE CHANGE IMPACTS: THE ROLE OF PALAEONTOLOGY

Determining climate change impacts on ecosystems: the role of palaeontology

Climate change is projected to change the ecosystems on land and in the sea at rates that are unprecedented for millions of years. The fossil record is an archive of responses to climate change at a global ecosystem scale. While records are often fragmented, there are time intervals which – when thoroughly analysed with quantitative data – can provide valuable insights into the future of biodiversity on this planet. However, the most commonly used approach to derive projections of how ecosystems will look in the future are experiments on living organisms. By their nature, experiments are unlike the real world and cannot capture the ability of organisms to migrate, select, and evolve. They are often limited to a select few species and drivers of environmental change and hence cannot represent the complexity of interactions in 'real' ecosystems. This review provides an overview of projected impacts on marine ecosystems including: (1) the range of neontological methods, observations and their challenges; and (2) the complementary information that palaeontologists can contribution to this global challenge. I advocate that, in collaborations with other disciplines, we should aim for a strong visibility of our field and the knowledge it can provide for policy relevant assessments of the future.

CLIMATE CHANGE IMPACTS: THE ROLE OF PALAEONTOLOGY

Rising CO_2 levels are expected to radically alter our planet. Increasing atmospheric CO_2 radically alters the Earth system, with projected implications for ecosystems worldwide (e.g., Turley *et al.* 2010; Pörtner *et al.* 2014). The oceans, which cover 71% of the Earth's surface and represent >95% of its habitable environment, are likely to be strongly affected. The increase in atmospheric CO_2 alters the physical, chemical and biological properties of the ocean such as temperature, pH, stratification, and oxygen and nutrient availability (Pörtner*, et al.* 2014). Indirect consequences of a warmer world are increases in sea level and storminess (Stocker *et al.* 2013). Climate models project warming of the average surface ocean of 3°C, a loss of oxygen of the subsurface ocean of 3%, and a decrease in net primary productivity of 8% under business-as-usual scenarios by the end of the century (Lefort *et al.* 2015). High resolution Earth system models predict that the rise in CO_2 will result in carbonate undersaturation in high latitude surface waters, with respect to aragonite, by the middle of the century (Orr *et al.* 2005). By 2050, using the same scenario, physical drivers of biology, physiology, and ecology in most of the ocean will be outside their background variability (Henson *et al.* 2017).

However, what is much less well understood than the physical changes, is their impact on biodiversity and benefits gained by humans from ecosystems, termed 'ecosystem services' (e.g., Turley*, et al.* 2010; Pörtner*, et al.* 2014). Ecosystem services include (1) provisioning services such as food; (2) regulating services that affect climate; (3) cultural services that provide recreational, aesthetic, and spiritual benefits; and (4) supporting services such as photosynthesis, and nutrient cycling (Millennium Ecosystem Assessment 2005). Amongst the most pressing questions concern physiological impacts on individuals (Pörtner*, et al.* 2014), how species change their

distribution, abundance and phenology (Edwards *et al.* 2001), if the consequences of these changes in fundamental ecosystem structure impact regulatory and provisioning services (Poloczanska *et al.* 2013), and whether or not species can use their natural plasticity or evolve (Collins *et al.* 2014) to dampen the impact of climate change (Lohbeck *et al.* 2012; Collins and Bell 2004). Quantifying the full range of natural responses to climate change remains a key challenge.

Our current knowledge is based on several lines of evidence. Responses to ongoing climate change show shifts in abundance, geographical distribution, and migration patterns of marine organisms (Edwards*, et al.* 2001; Beaugrand *et al.* 2002; Beaugrand and Reid 2003). Poleward displacement of plankton, making use of the new opportunities as warmer waters expand, has been as fast as 100s of km/decade (Poloczanska*, et al.* 2013). These species specific changes in range expansion result in changes in food web structures (Kortsch *et al.* 2015) thereby impacting fisheries (Cheung *et al.* 2013).

These observations are supported by model projections of significant changes in the distribution, biomass and maximum size of pelagic communities by the year 2100 (Lefort*, et al.* 2015). Biomass and maximum size is projected to increase in the high latitudes but decrease in low and mid latitudes, impacting on large species with high metabolic needs because of reductions in food availability (Lefort*, et al.* 2015). It has been found that 14% of the global ocean experienced important species turnover (defined as the sum of species invasion and extirpation). In this analysis, while 6% - 44% of the ocean, mainly in the tropics, is expected to experience reduced biodiversity (Beaugrand *et al.* 2015) biodiversity is predicted to increase in high latitudes.

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Observations in the field have been corroborated by the results of experiments in laboratories and mesocosms that help provide mechanistic understanding of the underlying causes (Pörtner, *et al.* 2014). These experiments revealed differential vulnerability across the life stages of sea urchins (Dupont *et al.* 2012), changes in energy allocation to physiological processes (e.g. muscle wastage in brittle stars at continued calcification (Wood *et al.* 2008)) and the importance of energy availability in resilience to climate change in mussels (Thomsen *et al.* 2010), to name but a few. These experiments highlight that not all species or processes have the same vulnerability and some are not impacted at all (Wall *et al.* 2015).

By their nature, short-term experiments lack realism and cannot capture the organism's ability to migrate, to select from a vast population size, and ultimately the evolution of the species. The experiments need to focus on short-lived organisms that deal well with the laboratory conditions. Adaptive evolution is more likely to occur in species with fast generation times and large population sizes, such as marine microbes (Krueger-Hadfield *et al.* 2014; Scheinin *et al.* 2015). Long-term, multigenerational experiments are rare (Lohbeck, *et al.* 2012; Collins and Bell 2004) and often limited to asexual offspring of species with extremely short generation times under simplified environmental conditions. The results of these experiments suggest that adaptive evolution increases resilience, thereby potentially reducing the size of the impact on the ecosystem (Collins, *et al.* 2014).

A complementary approach to assess impacts of climate change and to generate such mechanistic understanding is based on the fossil record, wherein climate change

events occurred at different rates and amplitudes (Hönisch *et al.* 2012). Therefore, the fossil record is an ideal test bed for model projections of changes of distribution, size, abundance and biomass. Marine sediments provide archives of biotic and climate variability in response to abrupt climate change that are recorded with high temporal resolution, good preservation and global distribution. They preserve a wealth of information including abundance, size, biomineralization, ontogeny and reproductive strategy (in some species), and migration and extinction. The ability to compare the open ocean with the coast, the surface with the deep ocean, the land and the ocean for a vast number of species holds incredible potential for the contribution of palaeontology to this ongoing debate. Exploiting the fossil record of environmental change and its biotic response will allow the rules governing biotic responses to climate change in the past to be identified, thus informing predictive models of the future.

Here, I will assess how past records of biotic response to climate change can contribute to quantifying impacts of future climate change in the next decades. I will start with the independent environmental framework necessary for such assessment and discuss the impacts of climate change on biogeography and calcification, with a focus on the marine microfossil record. Using the Paleocene Eocene Thermal Maximum (PETM) as a case study, I will highlight the power of an integrated analysis of climate data, modelling, and marine and terrestrial fossil records.

ENVIRONMENTAL FRAMEWORK

Interrogating the fossil record of climate change critically hinges on the accuracy of the reconstruction of the physical environment. Too often, circumstantial evidence is

used to derive the physical change without independent information. Over recent years many proxies have appeared that allow us to quantify, within their constraints, environmental changes (e.g., Henderson 2002; Hönisch*, et al.* 2012). There are two main approaches to reconstructing the environment: (1) climate proxy compilations based on biotic and abiotic information stored in the fossil record (Robinson *et al.* 2008; Dunkley Jones *et al.* 2013); or (2) climate models (Lunt *et al.* 2010b; Stocker*, et al.* 2013); and, ideally, there would be a combination of both (Lunt *et al.* 2010*a*; Tindall *et al.* 2010). For climate models, the desired geographical resolution (Bopp *et al.* 2013; Dutkiewicz *et al.* 2015) has to be balanced against the ability to run these models for thousands of years (Ridgwell and Schmidt 2010). Without clear data or model output to attribute a biotic change to an environmental driver, circular reasoning is not uncommon. Ecological niche models (ENMs) provide the link between the physical climate models and distributions of species. ENMs estimate a species abiotic niche by correlating a known species occurrence with spatial environmental variables (Guisan and Zimmermann 2000; Pearson and Dawson 2003). They have been widely applied to modern distributions, mainly in the terrestrial record (Walther *et al.* 2002). They allow the quantification of changes in the abiotic niche in the past and then project these into the future (Stanton *et al.* 2014; Waterson *et al*. 2017). For example, Waterson *et al.* (2017) assessed if the environmental niches of several species of planktic foraminifera were stable between the last glacial maximum and today and if, therefore, species compositions can be used to reconstruct temperature difference using an ecological niche model. The strength of the fossil record makes it possible to distinguish between total range (presence absence) and the optimal niche (in this case high relative abundances/large body size (Schmidt *et al.* 2004; Schmidt *et al.* 2006). While the total niche of the investigated foraminiferal species did not change much

from the last glacial maximum to today, the optimal niche was more susceptible to environmental changes (Waterson, *et al.* 2017).

CLIMATE CHANGE IMPACTS ON MARINE MICROFOSSILS

Marine microfossils are an ideal system for investigating response to climate change: (1) they are very sensitive to a changing ocean environment (directly in contact with the changing environment, as opposed to metazoans) and cannot regulate their body temperature; (2) they have no known predator and, as such, are likely to react strongly to the abiotic environment with less important biotic interactions; (3) they have enormous population sizes and very few apparent barriers to gene flow, enabling a very rapid evolutionary response to selective pressures; (4) some groups preserve their entire ontogeny in their shell; and (5) they have an excellent global fossil record spanning 200 million years, and have survived periods of major climate change of different rates and amplitudes. Every sample contains thousands of specimens that also record environmental information via proxies thereby allowing direct links between environment and the biotic response.

The fossil record of marine microfossils fossil spans multiple intervals of past rapid climate change over more than 100 million years (myrs). Today, marine microfossils have global distributions with clearly defined biogeographical zones suggesting strong environmental controls determined by a few dominant species. Their modern ecosystem functions ranges from primary production at the base of the food chain and the biological pump (phytoplankton) to carbonate and silicate production and therefore regulation of global biogeochemical cycles.

Biogeography changes

Changes in geographical ranges and abundance of microfossils have been applied to assess changes in climate in the past, most successful by CLIMAP (CLIMAP Project Members 1976) and its offspring the Margo project (Margo Project Members 2009). If combined with climate model that quantify the natural environment, these data can be used to interpret response to climate change in the past and project the future. We assume that plankton simply migrates without changes to their niche and this provides the foundation for using microfossil distributions in transfer functions for environmental reconstructions. Niche models, though, challenge the assumption of niche stability in foraminifers over the last 20 thousand years kyrs (Waterson *et al.* 2016).

The dominant signal in marine plankton to temperature changes is habitat tracking, i.e. an expansion of warm water species towards to pole in response to warming (Dowsett *et al.* 2012). Locally, this can lead to increases of warm water species in areas that previously did not support these species. For example, an annually resolved foraminiferal abundance record off the coast of California shows an increase in temperate/subpolar species over the last decades in response to the warming of the California Current (Field *et al.* 2006). Such high resolution records of response to climate change are rare but invaluable in assessing impact of environmental change.

Combining the physiological understanding with climate models predicting future temperature, food and light suggests decrease of foraminiferal abundance and diversity in the tropics and subpolar regions and increase in the subtropics and around the poles for the future (Roy *et al.* 2015); though the model does not consider the impact of carbonate chemistry changes especially in high latitudes. Such assumptions are testable at various temperatures in the past across glacial interglacial cycles with warmer time intervals during the Eemian for example.

Calcification response – regulatory ecosystem services

A fundamental ecosystem function of foraminifers and coccolithophores is carbonate production, which regulates biogeochemical cycles, and is determined by abundance, size and weight of a population. Calcification is an energy demanding process and projected to be strongly affected by changes in CO_2 (Kroeker *et al.* 2010). Marine plankton in the modern ocean precipitate around 50% of the marine carbonate (Schiebel 2002) with the other half being produced on the shelf by a wide range of organisms including corals, calcifying algae, and molluscs. Over the course of the Cenozoic, pelagic carbonate production was dominated by coccolithophores, whilst today both coccolithophores and foraminifers contribute similarly to overall carbonate production.

Mass extinctions in the fossil record highlight the long duration of reduced carbonate accumulation (Henehan *et al.* 2016; Hull *et al.* 2011) and hence likely production, raising concerns about the future. Mechanistic understanding of the drivers of

calcification is fundamental to forecasting impacts of climate change on calcification, the marine carbon cycle and feedback on the ocean CO_2 uptake.

The physiology of calcifying phytoplankton (coccolithophores) will be impacted in positive and negative ways. Photosynthesis will benefit from the higher CO_2 conditions, while calcification is projected to be negatively impacted (Bach *et al.* 2013). This mechanistic understanding of physiology derived in the laboratory can be tested in the modern Ocean (Beaufort *et al.* 2011) and fossil records (O'Dea *et al.* 2014). Globally, with increasing CO_2 in surface waters carbonate production in coccolithophores decreases (Beaufort*, et al.* 2011). A similar response can be found across the last glacial interglacial transitions but also highlights a high complexity of species specific reactions (Beaufort*, et al.* 2011; seePörtner*, et al.* 2014 for a recent discussion).

Carbonate production in foraminifers is driven by test size and thickness. Size in foraminifers is predominantly impacted by the optimal temperature of each species (Schmidt*, et al.* 2006; Schmidt*, et al.* 2004) and therefore fluctuates with the environment through time in a predictable fashion (Schmidt *et al.* 2003). Weight, reconstructed as size normalized weight (SNW), appears to be influenced by a wider range of parameters. The carbonate produced by an individual has been related to changes in carbonate saturation in experiments (Russell *et al.* 2004) with strong species specific sensitivities in field samples (Barker and Elderfield 2002; Osborne *et al.* 2016) although many environmental parameters in the ocean are highly correlated. Seasonally, even at places without strong changes in saturation, SNW

varies additionally in response to temperature and food availability again with species specific sensitivities (Weinkauf *et al.* 2016).

Such species specific responses to multiple stressors are difficult to disentangle in experiments today. Applying the fossil record of warming and acidification has the potential to provide significant advances in understanding (Osborne*, et al.* 2016) with examples focusing on the most recent glacial-interglacial cycle (Barker and Elderfield 2002) and in the Pliocene (Davis *et al.* 2013).

The *early Late Pliocene* (3.6 to 3 Ma ago) is an attractive target interval as it is the last extended interval in Earth history when atmospheric CO_2 was comparable to today (Seki *et al.* 2010) and global climate globally 3°C warmer. Pliocene SNW has shown that species react to the environmental changes associated with glacial-interglacial changes in deeper time and that their weight changes scale with the amplitude of climate change, i.e. a small Pliocene forcing results in smaller weight changes (Davis*, et al.* 2013). The shortfall of using this time interval is that it is: (1) a generally warmer world without the dramatic rate of change we currently experience; and (2) amplitudes of change were significantly smaller and therefore likely not stretching the environmental niche of the species as much.

The major strength of the fossil record though is not the assessment of individual species but the potential to combine pelagic studies with shelf species. Climate change, either due to natural decadal variability or anthropogenic change, has been shown to impact on Great Barrier Reef corals (De'ath *et al.* 2012), coralline algae (Halfar *et al.* 2011) and molluscs (Gazeau *et al.* 2013). Such skeleton-based

approaches can be applied to a wide range of species and time intervals. The simplicity of the methodology provides potential for comparative work and large-scale synthesis of data from surface and deep ocean and pelagic and neritic ecosystems. A combined assessment of the impact of climate change on such a wide range of calcifiers would provide invaluable insights into vulnerabilities and potential for future carbonate production. One such target interval is the PETM, one of the Paleogene hyperthermal events ~56 myrs ago.

RAPID CLIMATE CHANGE - PALEOGENE HYPERTHERMALS

A significant body of work over the last decade or so has concentrated on assessing the impacts of transient climate change events in the geological record with the most detailed examples stemming from the Palaeogene hyperthermals. These events are often associated with large negative carbon isotope excursions, indicating the addition of vast amounts of carbon to the global carbon reservoir (Kirtland Turner and Ridgwell 2016). The injection of the carbon over short time intervals led to transient warming (Dunkley Jones, *et al.* 2013) and ocean acidification (Hönisch, *et al.* 2012). The PETM is the best studied of the hyperthermal events in a series throughout the Paleocene and Eocene. The cause for the rapid climate change leading to these transient events is still under debate (see (Frieling *et al.* 2016)); it is likely to be different for each given their different timing with regards to external forcing (Zeebe *et al.* 2017).

The power of these events, especially the PETM, is the potential for integrated assessment across latitudes and habitats from the shelf to the open ocean but also

between land and sea. The focus of the scientific endeavour to this point was on determining the physical and chemical changes associated with the climate perturbation (see Zhou *et al.* 2016; Zeebe *et al.* 2016; Gibbs *et al.* 2016 for some recent examples), though the event was first recognised by its biotic impact on the deep sea ecosystem (Thomas and Shackleton 1996).

The migration of species towards to poles and species turnover can be seen in a wide range of organisms in the marine planktic ecosystem including foraminifers (Thomas and Shackleton 1996; Lu and Keller 1995), coccolithophores (Bralower 2002) and dinoflagellates (Sluijs *et al.* 2008; Crouch *et al.* 2001) with subtropical species reaching the latitudes that are today associated with polar systems. Changes in the seasonality of runoff (McInerney and Wing 2011) and increased weathering (Dickson *et al.* 2015) led to reallocation of nutrients causing responses amongst the phytoplankton (Gibbs *et al.* 2006), including blooms of groups associated with harmful algal blooms (Sluijs and Brinkhuis 2009) but also shelf dwelling benthic foraminifers (Scheibner *et al.* 2005).

The most profound impacts were recorded in the deep sea where 40% of benthic foraminifers went extinct, a group of species that showed resistance to the mass extinction at the KPg boundary (Thomas 2007). Those benthic foraminiferal species surviving the PETM had the ability to enhance their calcification relative to body volume (Foster *et al.* 2013). Intriguingly, deep sea ostracods show highly variable responses, some of which suggest that the climate change impacted the assemblages negatively (Steineck and Thomas 1996) while others suggest little change (Webb *et al.* 2009).

The strength of this time interval is that global assessments are feasible (McInerney and Wing 2011). While the terrestrial record often does not have the same temporal resolution or accuracy of age determination, the geological record of the PETM includes high resolution sections of terrestrial sequences with astronomically tuned age models (Bowen *et al.* 2015). Those sections show rapid large plant range shifts (Wing *et al.* 2005). The mammalian records show rapid increases in mean species body size and abundance of herbivores and frugivores (Clyde and Gingerich 1998) in response to immigration of cosmopolitan new taxa (Gingerich 2003).

The PETM is an excellent example, which shows that the current response to climate change over the last decades is driven by the same underlying universal principles as in the past and demonstrates that past events are, therefore, suitable to help predict the future. Comparing the Paleogene hyperthermals and their different amplitudes of environmental change (Jennions *et al.* 2015) holds potential for assessing the important of different amplitudes of climate change and the impact these have on both marine and terrestrial ecosystems.

OUTLOOK

Traditionally, the impacts of climate change are assessed by time-consuming taxonomic or geochemical analysis focusing on a region (Edgar *et al.* 2013) or globally within a specific time slice (Yasuhara *et al.* 2012). Rarely are different events compared and, when they are, only at a single location (Gibbs *et al.* 2012; Jennions, *et al.* 2015); this is due to the extremely time consuming work of species identification.

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A wealth of information could be assembled if scientists focusing on different fossil groups were to generate papers that cross traditional discipline boundaries. The power of comparing sets of events, while acknowledging our difficulties in aligning absolute dates, would provide insights into the importance of rates of change and the associated impact. Such a question, while fundamental to the size of the impact of future climate changes, is hard, and perhaps impossible, to tackle experimentally.

Selecting species with different ecologies will allow morphological changes to be linked to environmental drivers, and the sensitivities to these drivers to be tested against prior adaptation. Overcoming this regional or temporal limitation by generating global datasets covering several time slices that experienced different rates and ranges of climate change for a range of organisms has to be our goal for the next decade.

Palaeontology's contribution to the last assessment on impacts of and adaptation to climate change was highly visible in the summary for policy makers of IPCC Working Groups II (Impacts, Adaptation, and Vulnerabilities) 'Many terrestrial, freshwater, and marine species have shifted their geographic ranges, seasonal activities, migration patterns, abundances, and species interactions in response to ongoing climate change (high confidence)…While only a few recent species extinctions have been attributed as yet to climate change (high confidence), natural global climate change at rates slower than current anthropogenic climate change caused significant ecosystem shifts and species extinctions during the past millions of years (high confidence) (IPCC

2014).' In collaborations with others we should aim for a strong visibility of our field and the knowledge it can provide in more policy relevant assessments in the future.

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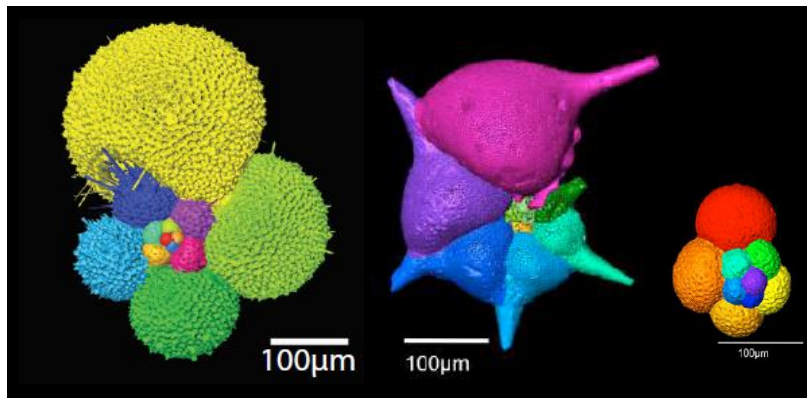
Figure 1: Developmental history of 4 species of planktic foraminifers reconstructed using tomography (Caromel *et al.* 2016) and unpubl. Data. From left to right: modern, Eocene and Paleocene specimen. Each colour represents a new ontogenetic stage.

Figure 2: Environmental changes (top) and associated biological responses (bottom) for the Paleocene–Eocene Thermal Maximum (PETM, left) and the industrial era (right) from IPCC AR5 WGII, Chapter 6 (Pörtner*, et al.* 2014). Episodes of largest environmental change are indicated with darker bands. Note the different timescale between the two columns. Both time intervals are characterized by rapid warming both on land and in the ocean: {modern: Wilson et al. (2006) and PETM: Kennett and Stott (1991)) and increases in CO_2 (modern: (Etheridge et al. 1996; Keeling et al. 1995) and PETM: (Zeebe et al. 2009; LOSCAR model); (Ridgwell and Schmidt 2010; Grid Enabled Integrated Earth System Model, GENIE model). For the recent industrial era, the Atlantic Multi-decadal Oscillation (AMO) is shown to highlight an example of high-frequency sea surface temperature fluctuations (Enfield et al. 2001) and their influence on marine biota. Note the species-specific calcification responses to climate change with decreases, increases, and high variability (coralline alga: (Halfar, et al. 2011); coral: (De'ath et al. 2009); PETM: (Foster, et al. 2013). While there was extinction

during the PETM (Thomas 2003), there is currently no evidence for climate-related extinction in the marine record. Warming led to migration of warm-water species into previous cold-water habitats (modern: (Field, et al. 2006); PETM: (Bralower 2002)). Pictures are examples of organisms highlighting the processes in each panel, and are not to scale.