Polar Oceans, Plankton and Oceanic Carbon Sequestration in a Warm, High pCO_2 World

a proposal to the MOPGA/DAAD

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1. Introduction - Links between future global climate change, Paleogene polar oceans, and the evolution of marine plankton

Future anthropogenic greenhouse gases are projected to reach levels not seen on earth for more than 30 million years: since the Eocene epoch (to pCO_2 equivalent concentrations possibly greater than 1,000 ppm e.g. IPCC scenarios RCP6.0, 8.5: Beerling & Royer, 2011; IPCC: Masson-Delmotte et al., 2013). Diverse methods based on projecting our current climate into the future (e.g climate models) are used to understand future impacts, but study of the Earth's climate as it existed in the high pCO_2 world in the Eocene, and how it differed from colder earth climates are also important research targets.

Ocean phytoplankton production, particularly by diatoms and coccolithophores, capture carbon. With their shells acting as ballast, they export (sequester) it into deep sea sediments. This process, the 'oceanic carbon pump', is critically linked to polar oceans. Sequestration occurs both in polar oceans and in lower latitudes, where nutrient rich intermediate waters, also largely originating in polar oceans (Sarmiento et al., 2004) are upwelled again by physical processes to drive phytoplankton growth. Study of Paleogene (the early Cenozoic, comprising Paleocene, Eocene and Oligocene) ocean export productivity and climate are thus major goals of the International Ocean Discovery Program (IODP Science Plan: Bickle et al., 2011).

The transition from the warm world to the more modern cold, glaciated world marks the end of the Eocene and the start of the cold Oligocene epoch. This transition (*Figure 1* - the 'E-O boundary', ca 34 million years [my] ago; Coxall & Pearson, 2007) is known to be linked to several other changes: a major drop in atmospheric pCO_2 (Beerling & Royer, 2011); the development of polar ocean circulation systems in the latest Eocene (Stickley et al., 2004; Lazarus et al., 2008; Egan et al., 2013); the initial formation of polar ice-sheets (DeConto & Pollard, 2003); and changes in global ocean export productivity (Schumacher and Lazarus, 2004). The changes in ocean export production across the E-O boundary have been inferred mostly by changes in bottom dwelling organisms (i.e. benthic foraminifera: Diester-Haas & Zahn, 1996). However the changes in phytoplankton responsible for this, and the links to changing ocean circulation are still very poorly understood. Diatoms first become diverse in the mid/late Eocene and it is widely assumed that increase in polar diatom abundance and productivity in the developing Southern Ocean played a key role (e.g. Egan et al., 2013). Studies of this time interval are thus important to understanding earth climate system and its sensitivity to high atmospheric pCO_2; and in particular, the role of phytoplankton and the ocean carbon pump in regulating climate.

Also important are changes in plankton ecology and diversity. Ocean carbon export depends not only on absolute productivity of shelled phytoplankton but also their relative abundance. Paradoxically (given their carbon-rich $CaCO_3$ shells), coccolithophore productivity, on time scales <10,000 years actually emits carbon dioxide back to the atmosphere, contributing to atmospheric pCO_2 rise (Rost & Riebesell, 2004). The export of diatoms to the sediments is thus crucial for future development of the carbon pump. Most diatom carbon export productivity is concentrated in species found in colder waters, and would decline as oceans warm (Bopp et al., 2005; Tréguer et al., 2018). It is also conceivable that some of these diatom species could become extinct, as preliminary analyses suggest they were not present in the only slightly warmer oceans of the earlier late Cenozoic, evolving first only when oceans cooled to near their present state (Late Miocene, ca 10 my ago; Lazarus et al., 2014). Extinction of important carbon pump plankton during the warm interval would have dramatic consequences for a post-anthropogenic-warming world. A system still holding rare cold-adapted species could rebound to full original functionality, but extinction would prevent

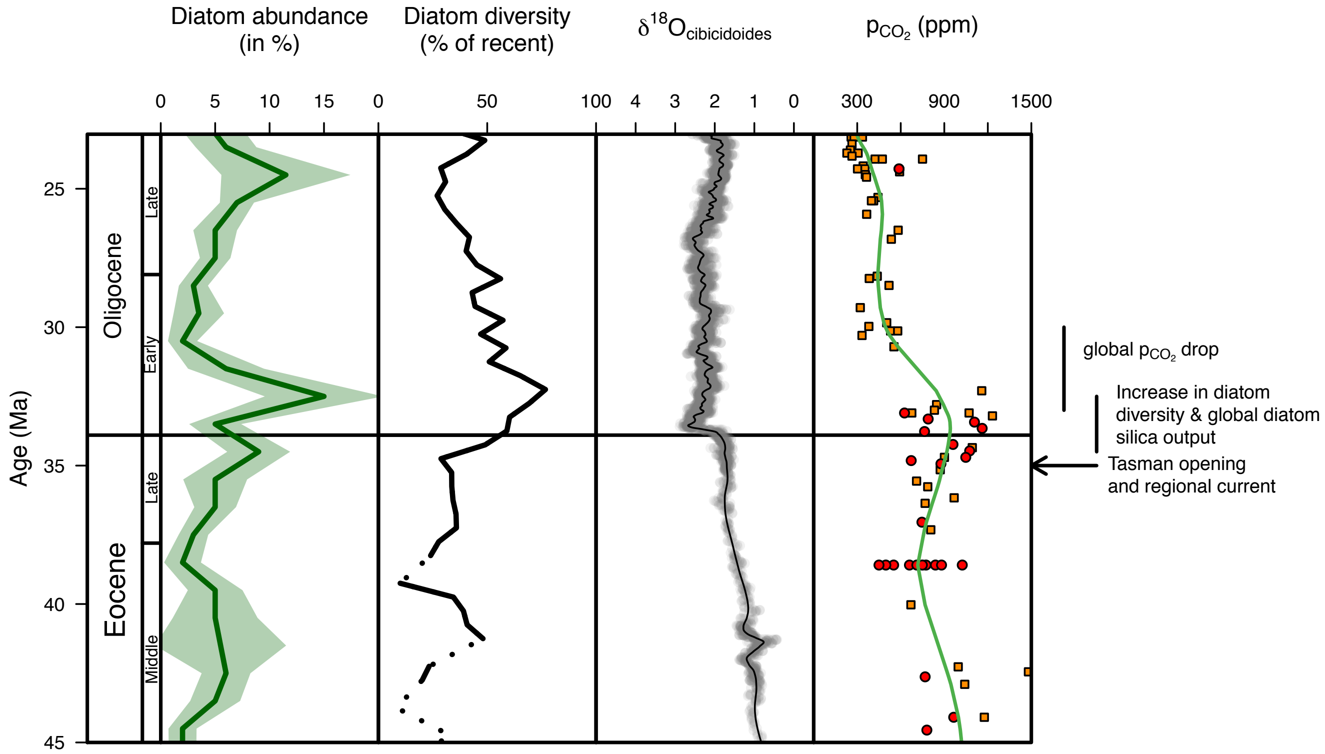

Figure 1 - Summary of Eocene-Oligocene marine diatom plankton & climate change trends. Diatom concentration in deep-sea sediments (simple average of data per time interval: Renaudie, 2016); Diatom species diversity (as % modern: Wiese et al., 2016); global deep-ocean climate ∂18O proxy (Zachos et al., 2008); atmospheric pCO2 concentration (Beerling and Royer, 2001; squares are phytoplankton-based proxies while dots are the other proxies). On right, diagrammatic summary of major events - regional gateway opening and Southern Ocean circulation initiation (Stickley et al., 2004); diatom and pCO2: data series shown this figure.

the system from recovering its original state. This could irretrievably reduce the pump's effectiveness and permanently impact global climate.

These observations taken jointly identify the importance of understanding how (polar) diatom production and diversity function in a high pCO_2 world. Our ability to predict future plankton, and particularly diatom biodiversity change from living systems though is limited by the extreme technical/logistical difficulty of studying open ocean ecosystems: observations are limited by short timescales, patchiness in coverage and taxonomic problems; while *in-vitro* systems cannot duplicate the complexity of the open ocean, such as water column structure. There is also the inherent problem of studying processes (extinction) which by definition, do not exist (yet) in still-living species. We thus do not have anything like ICU Red List understanding of these organisms. Studies instead mostly extrapolate shifts in latitudinal species (or more poorly resolved higher taxa) distributions, but encounter significant 'no-analog' problems in polar regions, as the key cold-adapted taxa are shifted into temperature/latitudinal regimes that do not exist in modern oceans (e.g. Thomas et al., 2012). By contrast, diatoms are known to have evolved dramatically between the mid Eocene and Oligocene, increasing in diversity and abundance, overtaking the radiolarians to become the primary silica export plankton of the oceans (*Figure 1* - Lazarus et al., 2014; Wiese et al., 2016; Renaudie, 2016).

These ecologic and evolutionary changes in fossil siliceous plankton, occurring at approximately the same time as ocean change across the Eocene-Oligocene transition, suggest that study of these groups' Paleogene biodiversity and abundance histories can yield insight into the links between evolution, climate change, ocean circulation, and plankton productivity in a high pCO_2 world.

2. Goals of proposed study

The basic model that we examine is: (tectonically driven) changes in ocean circulation+increases in weathering -> increased polar ocean areal extent, more ocean nutrients, and, via evolution, more polar diatoms -> increases in global plankton export productivity, particularly in high latitudes -> drawdown of pCO_2. Our project specifically poses three main questions (discussed below) which, if answered, can be assembled to test this model. Questions 1 and 2 specifically address the physical development of the oceans and their relationship to export productivity. Question 3 addresses the separate, but linked issue of how physical changes in ocean environments impact plankton evolution, and most particularly the risk of species extinction.

The questions are addressed by data generated from several work packages (radiolarian faunas; diatom floras; sediment composition and accumulation rates; carbonate geochemistry/benthic foraminifera accumulation rates; and ocean circulation and biogeochemistry modelling). Each work package is described in the following section '3', while in section '4' we explain how the data from the work packages will be assembled to answer each of our questions, and how these answers are relevant to current concerns about global climate warming.

Our proposed project complements current and planned IODP new drilling research. Specifically, Legs 371 and 378 target(ed) a broad range of Paleogene time intervals and science themes, primarily using carbonate rich sections from cool temperate environments from the southern Pacific regions. Our focus is on true polar siliceous plankton from a global set of locations, particularly our Atlantic transect, and our focus on just two themes - late Eocene-early Oligocene productivity change and evolutionary change in siliceous plankton, and will thus complement the more regional, carbonate-centered studies of other planned research. We will however cooperate with the siliceous plankton workers from these legs, particularly Chris Hollis' group (GNS, New Zealand) exchanging taxonomic and other information, and integrating data from their studies, as appropriate, into joint syntheses.

Our Questions:

1. *How much did the polar oceans, particularly the Southern Ocean, increase in areal extent between the Eocene and Oligocene, and was the areal expansion associated with the development of intermediate water transport from high to low latitudes?*

The polar oceans, primarily the Southern Ocean, are crucial to carbon capture, via high export productivity in the polar regions, and provision of nutrients to lower latitude high productivity regions. The origin and geographic extent of these oceans and particularly the Southern Ocean are thus essential pieces of information to understand Paleogene oceans and the carbon cycle. The literature on the origin and development of the Southern Ocean is large, complex, and discordant. Different types of observational data - continental breakup (gateway openings at the tip of South America and south of Australia, removing blocks to circumpolar circulation), benthic faunas, bottom water mass tracers, and surface water plankton give quite different results for the timing, from mid Eocene (50 my) to the Miocene (20 my) (e.g. reviews by Nelson & Cooke, 2001; Barker & Thomas, 2004). Computer circulation models (Barron & Peterson, 1991; Huber et al., 2004) suggest, given open gateways, Paleogene circulation geographic extent only moderately different from today, although these may be somewhat biased towards the modern, being developed from and calibrated to today's circulation. Multiple ocean drilling legs (=expeditions) south of Australia-New Zealand have constrained the gateway opening

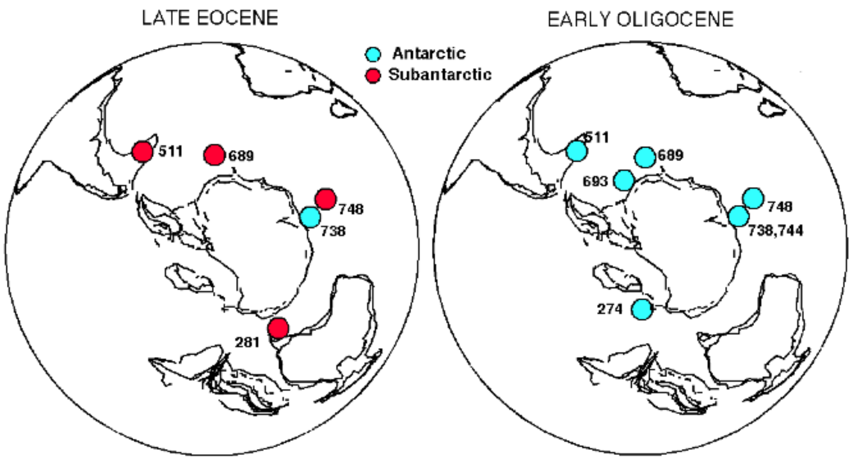

Figure 2 - Maps showing spread of endemic polar radiolarian biota in proto-Southern Ocean between late Eocene and early Oligocene, after Lazarus & Caulet (1994) and Lazarus et al. (2008). Age resolution is only ca 5 my and biogeographic interpretation of these Paleogene species was entirely subjective, based on authors' experience.

and timing of polar current origination there to the latest Eocene (significantly, slightly before global temperatures dropped and Antarctic ice sheets formed, supporting the idea that polar ocean productivity may have drawn down atmospheric pCO_2: Egan et al., 2013). In this region radiolarians (Pascher et al., 2015) and dinoflagellates were particularly useful, though the latter are found mostly in near-coastal sections (Stickley et al., 2004; Bijl et al., 2011), and are partially endemic even in the late Cretaceous, well before Southern Ocean formation, probably due to direct temperature control (Mohr & Mao, 1997). Southern Ocean geographic development elsewhere around the Antarctic is still poorly known. Temperature contrasts across ocean water mass fronts are fairly small vs geochemical temperature proxy precision, and they are thus are not well suited to mapping surface ocean water mass positions. Biogeographic methods are normally used. Carbonate microfossils (planktonic foraminifera, coccolithophores and discoasters) though give little information as they are mostly cool water cosmopolitan and/or low diversity in this time interval (Kennett, 1978). Early Eocene siliceous microfossils are either tropical or cosmopolitan (Sanfilippo et al. 1985; Asatryan et al., 2013). In polar regions cosmopolitan species are replaced by much more diverse, more useful endemic assemblages (i.e. specific to polar or subpolar regions) in the latest Eocene to early Oligocene (Lazarus et al., 2008). Diatom oozes, marking high diatom export productivity, dominate post-Eocene Southern Ocean sediments. These newly evolved siliceous assemblages have mostly though only been studied to identify a small number of 'biostratigraphic' (geologic age) marker species (numerous studies in deep-sea drilling Reports volumes). Nonetheless, initial biogeographic studies of radiolarians showed that they trace the growth of the polar oceans (*Figure 2* - Funakawa & Nishi, 2005; Lazarus et al., 2008). A more complete biogeographic survey by Pascher et al. (2015) confirmed the utility of radiolarian biogeography to trace polar ocean development, although their study is only for the New Zealand region and biogeographic assignments of species are based on a limited range of geographic locations (*Figure 3*). Paleogene polar diatom biogeography has not been substantially investigated.

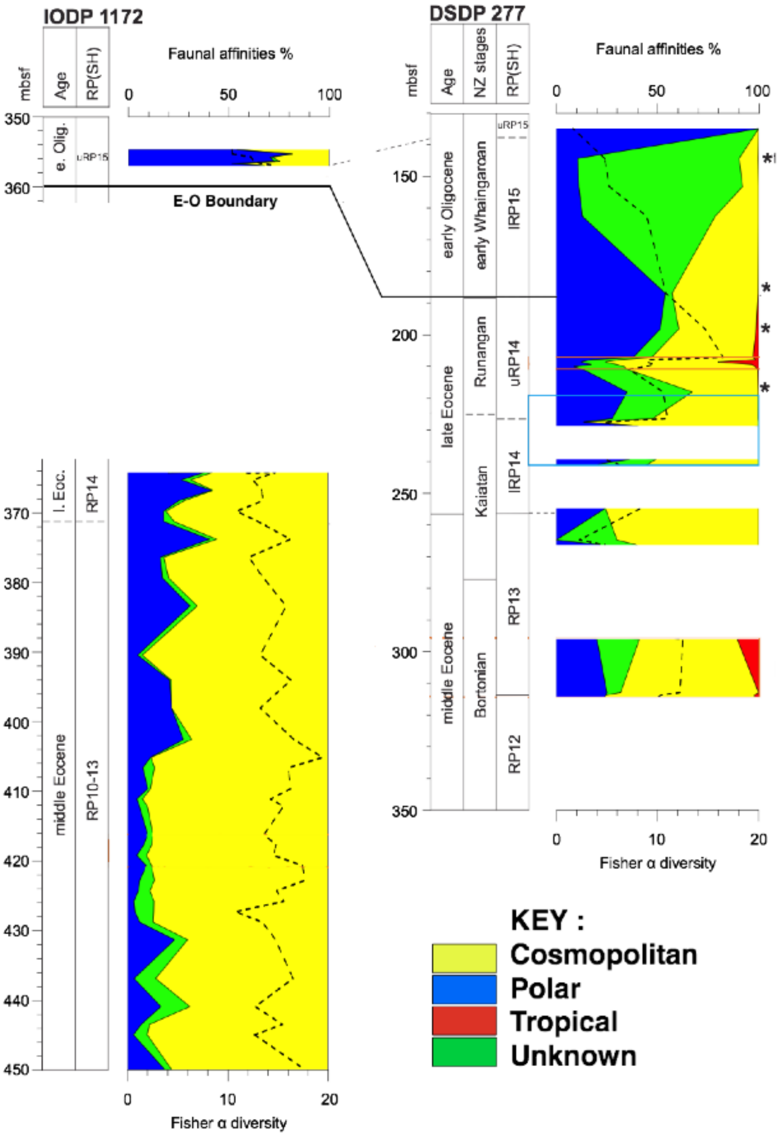

Figure 3 - Time series of Paleogene radiolarian fauna development in two deep-sea drilling site locations south of New Zealand, simplified from Pascher et al. (2015). Depending on meaning of 'unknown' (green) taxa, faunal change and implied Southern Ocean growth is either clearly in late Eocene (before) or mostly at/after after glaciation at E-O boundary. Unknown taxa are in taxonomically poorly understood radiolarian family Litheliidae, one of our targets for taxonomic study. Note also tropical species - tracers of warm surface waters transported to high latitudes in brief Paleogene peak warmth intervals (e.g. 'MECO' event at ca 300 mbsf in DSDP 277).

Northern polar oceans (Norwegian Greenland Sea) are known to have had distinct faunas and floras in the Paleogene but their extent and circulation are poorly known. One problem has been very poor geologic age control, but this has improved significantly in recent years (e.g. Eldrett et al., 2004 and subsequent papers), providing a new opportunity to improve our understanding of Paleogene paleoceanography in this region.

How either of these oceans were connected to lower latitude oceans via subsurface intermediate water circulation is largely unexplored, despite a substantial literature on Paleogene bottom water circulation, which documents cooling and spread from poles to tropical regions of bottom waters across the E-O boundary, concordant with glaciation of Antarctica (Zachos et al., 2001). In the modern ocean radiolarians can be used as tracers of intermediate water transport to low latitudes (Casey, 1993; Itaki & Okazaki, 2008; Boltovskoy & Correa, 2016). Similar insight into intermediate water nutrient transport in older time intervals, using radiolarians to reveal how polar nutrient transfer to low latitudes may have functioned in warm Paleogene oceans, however has not yet been done.

Methods: To understand polar ocean growth and intermediate water transport to lower latitudes we will use radiolarian and diatom biogeography, distribution of silica and carbonate sediments, and ocean circulation models (Work packages 1,2,3,4). Samples will be studied from around the Antarctic, and in latitudinal transects: one from the New Zealand sector of the Antarctic to the tropical Pacific, and one through the Atlantic, from the Weddell Sea to the Norwegian-Greenland Sea.

2. *How did ocean export productivity change between the Eocene and Oligocene; what role did enlarged polar oceans play in this, and how did the relative contribution of diatoms vs coccolithophores to export productivity change?*

Carbon export from an ocean is a product of area, which we address above, and rate of export per unit area. We will use several methods to estimate the rate of export of carbon into ocean sediments in our study sections, and how this changed between the Eocene and Oligocene. Additionally, not all plankton productivity is equal in the light of the carbon cycle: marine diatoms are today mainly responsible for the biological carbon pump and are the main carbon exporter to the deep sea (Smetacek, 1999). Calcareous nannoplankton (coccolithophores), while also contributing to the carbon pump, also add to the opposing alkalinity pump (i. e. they reject CO_2 to the atmosphere due to the precipitation of a calcareous shell; e. g. Frankignoulle et al. 1994). They thus have a different impact on the carbon cycle than diatoms, even if both, having mineralised ballasting skeletons, export carbon out of the system by sinking and trapping it in sediments. Change in the nature and composition of plankton productivity has thus direct consequences for the carbon cycle.

The different taxonomic group contributions to export productivity in the modern ocean are a complex global pattern due to the spatial heterogeneity of nutrient availability (*via* continental sources and ocean circulation) and seasonality. Diatoms account for half of ocean productivity, and areas of high diatom productivity are located primarily in areas rich in silicic acid: the Southern Ocean, the North Pacific and the Eastern Indian Ocean, estuarine areas, as well as upwelling areas in the middle latitudes. In the early/mid Eocene however, diatoms were still a relatively rare group with low diversity, abundance or geographical spread.

Prior studies have shown that it is just before the Eocene-Oligocene boundary that diatom diversity (Lazarus et al., 2014) and abundance (Renaudie, 2016) began to rise (*Figure 1*). Further, low-resolution, preliminary studies show that the locus of their rise to abundance was restricted to the high latitudes (Renaudie, 2016), matching prior observations of coeval increased productivity in the Antarctic (e. g. Diester-Haass, 1995; Salamy & Zachos, 1999; Schumacher & Lazarus, 2004). Similarly there is evidence for changes in nutrient sources and transport in the Southern Ocean during this period with the opening of ocean gateways (Stickley et al., 2004) and the erosion of the Antarctic continent by the build-up of the East Antarctic glaciation (Ehrmann & Mackensen, 1992). Hence the idea that the creation of the modern biological carbon pump is linked to Eocene-Oligocene changes in ocean extent and nutrient availability in the Southern Ocean. Initial studies on diatom productivity however are based on syntheses of scattered, heterogenous, low precision, previously published data, which has not been placed in a clear paleoceanographic circulation framework.

Methods - To estimate rates of export productivity and the relative contribution of siliceous vs calcareous phytoplankton, we will use microfossil accumulation rates (i. e. biogenic opal and biogenic carbonate accumulation rates), accumulation rates of benthic foraminifera, carbon isotopes in planktonic and benthic foraminifera, and silicon isotopes on selected radiolarian species, in the two latitudinal transects (Work package 3). In addition to this, a synthesis of published data on biogenic opal and carbonate accumulation rates will complement these data by framing them in a global context: specifically, the full dataset will be used to constrain an ocean circulation model of export productivity (Work package 4).

3. *What effect did these changes in polar ocean environments have on the evolution, and particularly speciation and extinction, of species of siliceous plankton? Are major changes in ocean temperature or productivity associated with significant extinction events in these groups?*

Understanding species-level behaviour is essential to understanding how plankton controlled ecosystem services such as the carbon pump will respond to anthropogenic climate change. Two crucially different behaviours need to be understood - changes in abundance, a presumably reversible (post warming) ecologic response, and extinction. Evolutionary recovery of ecosystem function via speciation, after substantial extinction, is known in plankton to take several 100 kyr to several my (e.g. D'Hondt et al., 1998), thus extinction of carbon-pump significant species during a global warming phase would effectively permanently alter ecology and system services. The E-O transition is the only climatic event in the geologic record similar in magnitude (based on pCO_2 values) to projected future warming, since planktic diatoms first radiated abundantly in the late Eocene. Although ideally we would prefer a large cold to warm climate event, climate history since the late Eocene is mostly one of step-like cooling with only minor warming events. Thus, we specifically want to determine both abundance changes, and evolutionary changes in siliceous plankton in response to the major temperature change across the E-O time interval. Did dominant species decline in abundance but persist, albeit as rare species? Or did they actually become extinct, thus permanently altering the ability of the biota to restore? Did cold-water adapted species actually evolve first in the warm late Eocene, and only increased in abundance with cooling in the Oligocene, suggesting that 'cold' species can actually survive in warmer conditions? Initial studies suggest major changes at the E-O at the ecologic and evolutionary level in both diatoms (Fenner, 1985; Lazarus et al., 2014; Barron et al., 2015; Wiese et al., 2016) and radiolarians (Sanfilippo et al., 1985; Lazarus et al., 2008; Moore et al., 2008), but these are mostly based on regional data (which cannot evaluate migration or persistence of refugia), small sample sizes, or are restricted to the (small) subset of species used as biostratigraphic age markers.

Methods: To answer these questions robustly we will taxonomically characterise all species in the faunas and floras, collect comprehensive occurrence data in time series of samples globally distributed in different environments, and from these data determine and distinguish ecologic and

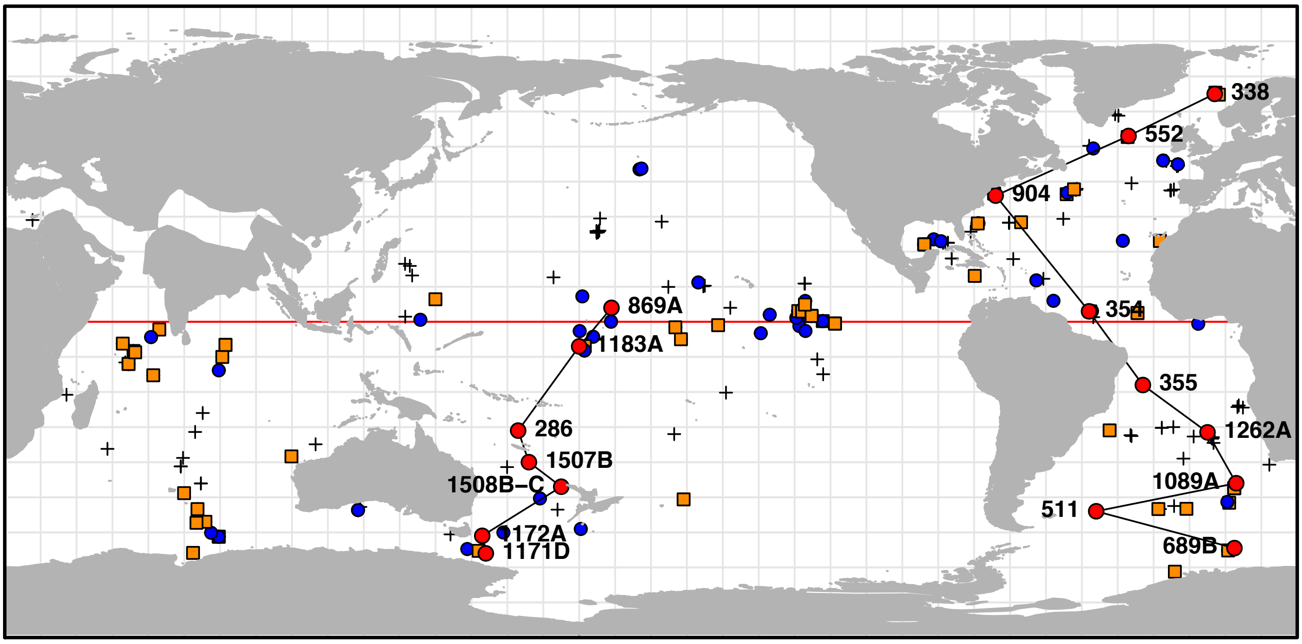

Figure 4 - 35 Ma paleo-position map showing primary latitudinal siliceous biota transect sites (connected red dots), other well characterised deep-sea drilling sites with silica biotas and age control in the NSB database (orange squares), less well studied silica sites (blue dots) from the MRC database, and sites with carbonate for accumulation rate analyses (crosses).

evolutionary responses - particularly extinction - to matched histories of environmental change. Data and results from all work packages will be integrated for this part of our study.

3. Work packages

WP1 - Sampling and age control

There are many sections available for our study that contain siliceous biotas (*Figure 4*). Those selected for inclusion in our NSB database have detailed biotic lists, although mostly for geologic age markers, and recently revised age models for geologic age. Age models are continuous lines fit to available section specific age control data that relate depth in a geologic section to geologic age, and are standard for paleoceanographic research. The NSB database, run by us, houses the world's most extensive (>400 sections), curated age model library for deep sea sections. A subset of the NSB sections (connected red dots) are selected for latitudinal transects (poles to equator), and include new Sites drilled by recent Leg 371, on which Asatryan sailed (Sutherland et al., 2018). Time series of samples from these will be used to study development of biogeography/ocean circulation boundaries, transport of intermediate waters to low latitudes, and evolutionary response of biota to climate change. Several additional sites are currently under revision by the international community (P. Bown, pers. comm. 30.1.2018); we will make use of these new age estimates as available. Other NSB sites, some with older age models, plus selected less well studied sites (locations used to make taxonomy reference slides for the international Micropaleontology Reference Centers [MRC] project, which the MfN leads) will be re-examined as needed using rapid 'smear-slide' based biostratigraphy of coccolithophores and diatoms to identify locations for improving geographic control in biogeographic analyses, and to improve coverage in sediment accumulation rate work (single samples in time slices). All samples will also be checked for adequate preservation of microfossils, and reworking (contamination by older material). One student will carry out this initial biostratigraphic survey, with sample preparation by MfN lab tech Fr. S. Salzmann. These data, together with stratigraphic data from radiolarians in the selected sections, will be used for new age models (using our custom age modelling program ADP: http://github.com/plannapus/NSB_ADP_wx/releases). Calibrated, partially regionally tuned zonations for all groups are available (e.g. Hollis et al., 1997; Varol, 1998; Barron et al., 2015; Gradstein et al., 2016) and will be mapped to the current reference age scale (Gradstein et al., 2016). Sample information and age models will be held in the NSB system. Sampling resolution will vary according to goals: 1 my resolution for initial work and significantly higher resolution across selected key time intervals and geographic locations (stepwise to ca 100kyr), particularly in our transects to clearly resolve timing of system component behaviors and thus clarify probable cause and effect relationships. Age models also are the base for calculating accumulation rates (WPs 3 and 4). We think we can obtain an accuracy to calculate useful rates at 0.5 my resolution in geographic maps, and at ca 0.1my resolution in time series across key transition intervals. Sampling will match available manpower, with 200-400 samples chosen in total per analysis/proxy, depending on time each required per sample.

WP2 - Mapping ocean development and determining extinction risk using siliceous microfossils

Radiolarians and diatoms are siliceous protist plankton that dominate the preserved microfossil record in Cenozoic polar regions. The photosynthetic diatoms are one of the main exporters of carbon into bottom sediments ('sequestration' of cellular organic carbon), primarily by 'ballast effects' - either thick shelled, fast sinking cold water species, or by seasonal 'blooms' that create aggregates (mats) that are heavy enough to sink rapidly to the sea-floor. Their living plankton diversity is very large but only ca 50 or so species are found in typical sediment samples. Radiolarians are much more diverse (up to 200 species in single fossil sample); their cells are very large and are often functionally mixotrophic (zooplankton but with algal symbionts). Their fast sinking cellular remains play a secondary, although significant role in global ocean carbon export (Lampitt et al., 2009; Biard et al., 2016). Bulk accumulation rates of these, and carbonate plankton, are studied together with other, geochemical proxies of ocean export productivity in work packages 3 and 4.

In this module we make use of the extremely close correspondence of radiolarian (and to a lesser extent, diatom) species biogeography and ocean water masses/circulation (Hays, 1965; Moore et al., 1978) to map out Eocene-Oligocene polar ocean development and connections to lower latitudes. Microfossil biogeography has been used in seminal studies of Pleistocene climate change (e.g. CLIMAP project members, 1976). A different but analogous set of species has been used to map Eocene and Oligocene polar water mass development (*Figures 2 & 3*: Lazarus et al., 2008; Pascher et al., 2015). We will also use, for the first time, the occurrences in low latitudes of species primarily common in polar regions as tracers for intermediate water transport.

Available paleoceanographic studies of polar radiolarians have significant limitations. Although polar Paleogene radiolaria undergo major evolutionary turnover at ca 35 my within the late Eocene (prior pCO2 drawdown), their geographic extent and abundance in the sediment, and thus the extent of the Southern Ocean in the late Eocene is still poorly known. Only Pascher et al. (2015) have published such data but only regionally. Further, published studies have other problems:

One problem is our very limited knowledge of biogeographic affinities of individual species. The relative abundances or even presence at each location in an ocean environmental transect - basic data to determine the biogeographic signal of a species - are well known for only ca 10% of the Paleogene faunas or floras. Published lists of biogeography for species are mostly based on very few localities (Pascher et al., 2015), or (Lazarus & Caulet, 1994; Lazarus et al., 2008) are purely subjective. Because of a focus on stratigraphic forms or common species (e.g. Nigrini et al., 2006; Kamikuri et al., 2002; 2012), most published taxonomic surveys of mid latitude or tropical sediments are not a reliable guide to even the presence or absence, let alone abundance of (described) polar species. Further, most prior studies have looked only at the >63 μm size fraction, while many polar radiolarians are smaller, primarily found in the 45-63μm size interval (Plagiacanthidae, Artostrobiidae, Trissocyclidae and others: Renaudie and Lazarus, 2013). We will address these problems by examining numerous samples (>45 μm fraction using standard preparation methods e.g. Renaudie and Lazarus, 2013) at each time interval, from a full range of environments. We will in particular cover the entire circumpolar Antarctic, N-S transects in the SW Pacific, S Atlantic, and, for north polar oceans, in the Norwegian-Greenland Sea (see work package 1). We will count the abundances of (almost) all the species present in these samples. Radiolarian diversity is high and consequently, as true in virtually all biosystems, most species are uncommon or even quite rare. We will thus use an 'extended' counting procedure with our own custom counting software Raritas (http://github.com/plannapus/Raritas) of counting first all taxa, then switching to a 'rarer taxa only' mode. This method was employed successfully by us in a prior study of the younger radiolarian faunas from the Antarctic (last 20 my: Renaudie & Lazarus, 2013). From this data - ca 10,000 specimens/sample, which should recover ca 90% of species in a sample (Chao & Jost, 2012) - we can employ the same interpretative strategy used in the CLIMAP work: the preferred environment of species can be determined, and from the composition of species in samples, the water masses they represent can be inferred.

The other problem is the poor state of radiolarian species taxonomy, which makes it very difficult to understand species biogeographic distributions. Many E-O species are not even described, and the use of described species names in published studies is inconsistent. Many species belong to groups such as Litheliidae, Pyloniidae or Spongodiscidae with complex, poorly understood morphologies. Taxonomic ignorance of these taxa directly impacts our ability to reconstruct polar ocean development (in *Figure 3*, the 'unknown' taxa are indeed litheliids). Diatoms present fewer taxonomic problems. Though they have not been intensively studied, their morphology is simple and diversity only moderate, thus a reasonable taxonomic framework at least partially already exists (e.g. Sims & Ross, 1988). Fortunately we are now able to address the radiolarian taxonomic problem efficiently.

A revolution in radiolarian taxonomy - Taxonomy, for our study, targets not evolutionary relationships between taxa ('systematics') but species descriptions to define taxonomic 'units' for ecologic work. For this, the variation (in fossils) of specimen morphologies are sorted into species-level groups. Descriptive radiolarian taxonomy has been radically transformed in recent years by several technologies. One is the spread of high quality, affordable digital imaging and image management systems (multi-megapixel cameras and matching computer screens, and supporting hardware and software). Images are central as Cenozoic radiolarians are too small to physically sort, and specimens are only briefly visible as they are viewed by scanning through microscopic preparations, each typically with ca 10K specimens. It is now possible within a single study to take, sort, and evaluate the needed imagery - 10K+ images: ca 2-4 images (at different focal planes) each of at least a dozen specimens of each species, for each the several hundred, many undescribed, radiolarian species encountered in a paleoceanographic study such as ours, that covers several my of time and different environments. Another are comprehensive, searchable taxonomic references: museum collections, online taxonomic species catalogs, and searchable pdf literature archives that make it possible to quickly match morphologies to published names. Lastly, major improvements in our ability to image and understand key radiolarian morphologic characters via tools such as µCT allow us to resolve the taxonomy of difficult groups. This latter point is particularly important to our project as, as noted above, many common (mostly larger) polar species belong to such groups. In these groups, although in principle sufficient external characters exist to use for routine species identification, the meaning of the characters cannot be determined as most of the relevant morphology is hidden inside a shell so complex that a clear image cannot be obtained, even with the near-transparent shells of Cenozoic radiolarians. Using µCT (micro computed tomography, a methodology which, other than to test technology (e.g. Wagner et al., 2015) is new to Cenozoic studies) the internal structures can be clearly imaged (*Figure 5*; Wagner et al., 2015; Asatryan et al., 2017), the taxonomy clarified, and these taxa then properly interpreted in applied paleoceanographic work.

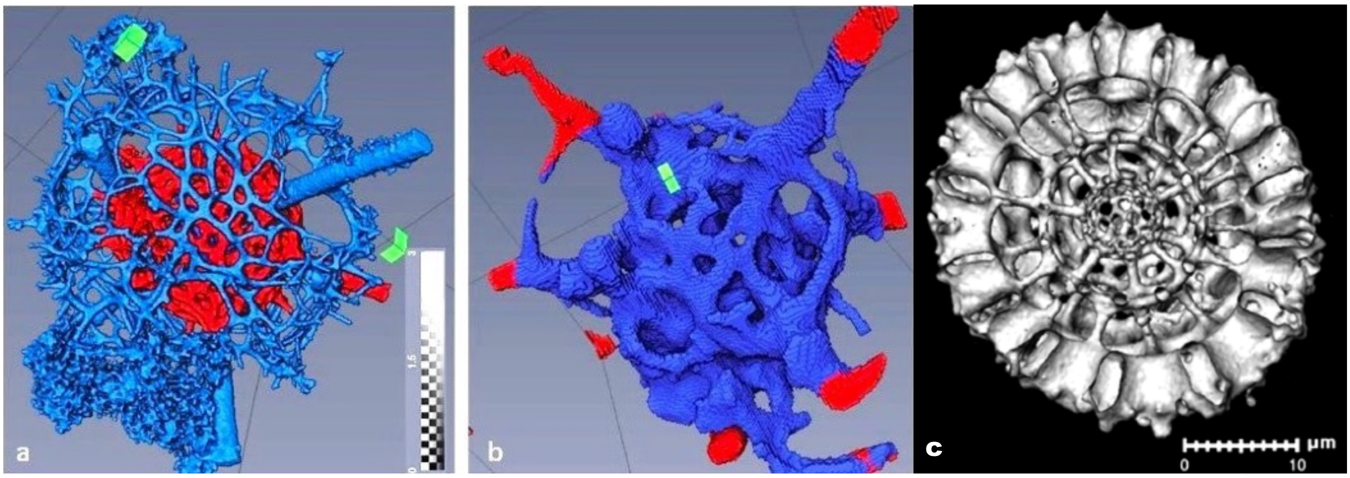

Figure 5 - µCT images of radiolarians. a & b) internal structures of Paleozoic radiolarian showing ability to resolve complex internals; c) cross-section of Eocene radiolarian; the massive outer shell fully obscures internal structure in light microscopy but is fully visible in this µCT image, created to test technology. a,b: Asatryan; c) Wagner et al. (2015).

We will employ all the above methodologies to thoroughly revise and improve Eocene-Oligocene polar radiolarian taxonomy. We have substantial experience in these new methods through our prior work (Renaudie & Lazarus: 2012-2016; Asatryan: 2017). The MfN will supply all needed microscopes (light and SEM), access to the MfN µCT, use of Amira workstations and computing clusters, and use of the unique MfN radiolarian fossil collections (Ehrenberg, MRC, and Lazarus' own collections: see https://www.museumfuernaturkunde.berlin/en/forschung/sammlungen/micropaleontology; https://iodp.tamu.edu/curation/mrc.html). We budget for external access to a special high resolution machine for imaging selected species with particularly fine morphologic features, and a single high performance GPU workstation for our group for local CT imagery analyses, avoiding potential access bottlenecks with the MfN shared facility (this workstation will also be user later in the project for climate modelling: see work package 4).

Calculation of diversity, speciation and extinction rates - For each time interval (depending on samples/sections used, from 500kyr to 100kyr) diversity, speciation and extinction rates, with confidence intervals, will be calculated from pooled occurrence data of all samples with the appropriate time resolution in a biogeographic region. Standard procedures in paleobiology including subsampling, resampling, Monte-Carlo, jackknifing; range-through, boundary crossers and others will be employed (Alroy & Hunt, 2010; Renaudie & Lazarus, 2013). Outliers and reworking will be identified using standard biostratigraphic methods of within-section continuity and between section consistency rules.

WP3 - Tracking changes in nutrient availability and plankton productivity using biogeochemistry

The aim of this work-package is to use established geochemical and sedimentological proxies to quantify nutrient availability, transport and export during the studied time interval. Specifically, $\delta^{13}C$ isotope ratios measured on foraminifera shells are linked to the $\delta^{13}C$ of dissolved inorganic carbon (DIC) in the water in which the specimen grew (Curry et al. 1988). This in turn depends on e.g. local productivity, water mass mixing and available DIC. Measuring $\delta^{13}C$ in benthic and planktonic foraminifera thus informs us about local productivity and carbon export to the deep-sea. While $\delta^{13}C$ is a well-established paleoclimatologic tool, silicon isotopic ratios of biogenic opal are much more recent and novel (De La Rocha et al., 1997; Hendry et al., 2014), but also illuminate local productivity and dissolved silica use in the water column (e.g. Egan et al., 2012).

Accumulation rates of microfossils (radiolarians, diatoms and benthic foraminifera) are a well-established tool used to estimate nutrient export. Siliceous microfossils (radiolarians, diatoms; and rarer taxa e.g. silicoflagellates and ebridians) are the only output of the marine silicon cycle, making their combined accumulation rate an estimate of silica, and silica-bound organic carbon, export (e. g. regional, Paleogene equatorial Pacific: Moore et al., 2008; global Cenozoic: Renaudie, 2016). Benthic foraminifera accumulation rates (BFAR) have been used for decades as a proxy for bulk organic carbon export (e. g. Herguera & Berger, 1991; Diester-Haass, 1995). Diatom and radiolarian accumulation rates will be computed along both transects, based on absolute abundance measured on smear, and sieved/random settled slides. This will be used, in addition to quantifying silicon export, to quantify the relative contribution of radiolaria vs diatoms to silica export (i. e., secondary vs primary producer).

Carbonate chemistry ($\delta^{13}C$ and $\delta^{18}O$) will be analysed on planktic and benthic foraminifera picked from the samples from the two transects. Measuring isotopes on both planktics and benthics will allow us to access the vertical carbonate chemistry pattern, in addition to the latitudinal pattern from the transects. While $\delta^{18}O$ provides a temperature/salinity framework, $\delta^{13}C$ will be used to quantify carbon export. Prof. Dr. U. Struck (MfN) has agreed to provide training in identifying benthic foraminifera and performing isotope analyses to one of the two PhD students.

Additionally, as a second line of evidence on productivity, phosphorus accumulation rates (see e.g. Filipelli, 2008) will be measured in part of the transects, as a collaboration with Dr. Martin Schobben (University of Leeds).

Lastly silicon isotopes ($\delta^{30}Si$) will be measured on a small number of selected radiolarian species representative of surface, intermediate and deep water along the South Pacific transect. Forty (ca.) specimens per species, per sample will be picked by us and analysed by our collaborators, Patrick Frings (GFZ-Potsdam) and Guillaume Fontorbe (University of Lund). Prior studies (e.g. Fontorbe et al. 2016, 2017) showed the usefulness of this proxy to quantify the concentration of dissolved silica in past water masses as well as the amount of it being recycled due to biological activity (i. e. siliceous microfossil productivity). The use of single-species isotopic analyses follows results of a pilot study between our team and Drs. Frings/Fontorbe (Renaudie et al. 2017): the goal is to eliminate potential vital effects, and also to recover a depth-specific signal. Depending on the abundance of diatoms in lower latitude samples, we will also consider analysing a few diatom species for silicon isotopes as well: radiolarian-based silicon isotope analysis is a relatively new proxy, while diatom-based analysis is more established and could provide a sanity-check (a second line of evidence) on the surface-water radiolarian results.

WP4 - Global syntheses and modelling

While WP2 will give us site-specific biogeography/water mass data and WP3 site-specific nutrient export data along N-S transects, both need to be integrated into a global circulation framework in order to give us a realistic picture of the global oceanographic and climatic significance of the Eocene-Oligocene reorganisation of nutrient transport and export.

To achieve this, in addition to the data we will have accumulated in the two transects (microfossil biogeography and accumulation rates; carbonate and silicate geochemistry), a global synthesis of published data on biogenic opal and biogenic carbonate deposition will be conducted. This will provide complementary, albeit much lower-resolution, data for many of the Eocene-Oligocene ocean areas not covered by the detailed new data generated in our study. Both types of data will serve as calibration points for an Oceanic General Circulation Model (OGCM) – possibly MITgcm (Hill & Marshall, 1995; Marotzke et al., 1999; Adcroft et al., 2002), along with packages GCHEM and DIC, or GFDL gcm (Manabe et al., 1991) – to model latitudinal nutrient transport and biological productivity at the different steps of the sequence of events near the Eocene-Oligocene boundary. OGCMs (including the MITgcm) have been successfully used in paleoceanography and paleoclimatology in the past, in the Cenozoic (e. g. Huber, 2002; Huber et al., 2003; Haines, 2012) as well as in older time intervals (e. g. Brunetti et al., 2015; Pohl et al., 2017). Our knowledge of Eocene and Oligocene paleogeography (e. g. Seton et al., 2012), paleotopology/bathymetry (Baatsen et al., 2013), ranges of basic climatic conditions (temperature, Zachos et al. 2008; atmospheric pCO_2, Beerling & Royer, 2011), etc. is nowadays realistic and well-documented enough to set up proper initial and boundary conditions for the simulations.

Modelling will be carried on primarily by J.Renaudie using our new (budgeted) dedicated workstation for configuration/set-up runs and the MfN cluster computing server for full runs (currently 512 Xeon-class cores, 4TB RAM, 135 TB disk capacity; MfN assistance by Prof. K. Wünnemann's group). Dr Feulner (Potsdam-Institut für Klimafolgenforschung) has agreed to help us with set up (e. g. boundary and initial conditions) and continuing advice for these OGCM simulations.

4. Data integration: answering the questions; relevance to current global warming concerns

To test the model of paleoceanographic change, change in diatom productivity, and draw-down of pCO_2 we will mostly use relative timing of patterns. As noted in the proposal previously there is already a hint that polar oceanographic change at ca 35 my slightly preceded both diatom (and radiolarian) diversification and diatom opal accumulation in sediments, and that both of these slightly led the (admittedly less than perfect) record of pCO_2 decline in the early Oligocene. With our data on the geographic extent and opal accumulation of the nascent Southern Ocean, other proxies of nutrient use and organic carbon export, plus complementary data from both the tropics and northern Atlantic we will be able to test if the formation of a substantial global plankton carbon pump, driven by changes in polar regions, preceded the observed global drop in the earth's atmospheric pCO_2.

The knowledge delivered by our study will directly address concerns about current global warming. It will characterise how polar plankton and the carbon pump functioned in a much warmer, high pCO_2 world, similar to that projected for an anthropogenically warmed earth. It will provide a real world observation of how substantial the changes in plankton export were, be that could potentially impact global climate in the future. Further, our biodiversity data will tell us if major evolutionary changes, particularly extinction of climate-sensitive carbon pump species, might be expected in a climate transition on the scale of the Eocene-Oligocene, and thus by implication for our future planet.

There are of course limitations to our study, the most important of which is temporal scale. With the manpower and time available we cannot sample at much below 100,000 year resolution, which obviously means that a direct, one-to-one use of our results in future climate change prediction is not possible. Further, we implicitly assume that changes from warm to cold (our data) can be used by inversion to understand change from cold to warm. This assumption of symmetry, though not provable, seems reasonable. Nor do we attempt to quantitatively model carbon fluxes and climate. Although this would be valuable, we first need to establish the basic validity of the model, and we do not have the resources to also attempt this in the current study. Despite these limitations, our results will characterise equilibrium states for a complex, and crucial part of the global climate system which, due to limited baselines and other problems, cannot be easily determined using only modern data.

5. Collaborators and Choice of Host Institution

External collaborators -

Georg Feulner, PIK, Potsdam. Dr. Feulner is an expert in modelling past climates, and has agreed to advise and support us on setting up a realistic ocean circulation model for our project.

Paul Bown and Jeremy Young, UCL, London. Experts on Cenozoic coccolithophores, both have agreed to support our work on coccolithophore biostratigraphy, particularly taxonomic advice.

Jakub Witkowski, Szczecin, Poland (near Berlin) is one of the few other world's experts in Paleogene diatoms. Although Renaudie is also an experienced worker on these fossils, Dr. Witkowski can be consulted if needed on taxonomy.

Patrick Frings, AWI, Potsdam. Dr. Frings will collaborate with us running silicon isotope measurements using the AWI facilities.

Martin Schobben, University of Leeds. Dr. Schobben will collaborate with us by measuring P accumulation rates on some of our sites as a second line of evidence on paleo-productivity.

Chris Hollis, GNS, Wellington, NZ. Dr. Hollis' group are working on Paleogene radiolarians from South Pacific sites, including recent/upcoming IODP Legs. We will exchange taxonomy, and occurrence data for joint analyses.

Host Institution - The Museum für Naturkunde in Berlin (MfN) is one of only two institutions in Germany with Cenozoic radiolarian specialists. Drs. Lazarus and Renaudie, uniquely, have extensive experience in both paleoceanographic and paleobiologic research, polar and tropical oceans, and the underlying methodologies of the proposed study (modern digital taxonomy, geochronology and age modelling, quantitative faunal studies, geochemistry of silica systems). They also both have significant experience with diatoms: Renaudie et al. (2010), Lazarus et al. (2014); while Lazarus has worked with the diatom research community for >20 years as curator of the Ehrenberg diatom types collection. The MfN offers unique resources including the modern MRC and historic radiolarian type collections, and the NSB database. Dr. Lazarus also heads a new community project to create a Cenozoic online radiolarian catalog which will be used for the planned taxonomic work. The MfN has numerous facilities with access at no charge to this project including LM and SEM microscopes, µCT and Amira workstations, and fully equipped micropaleontology and stable isotope labs. The MfN is located in Berlin, with a rich landscape of nearby special research facilities, libraries and universities (including our ocean model collaborator at PIK), and is relatively near the deep-sea drilling core repositories and other facilities of Germany's marine research institutions in Kiel, Bremerhaven and Bremen. Lastly, the MfN provides an unusual opportunity for a climate research group to use a full panoply of established education and outreach resources to communicate climate change science to the public and, being in Berlin, to political decision makers.

6. MfN Team and workplan

Our team will consist of 2 postdocs (Drs. Asatryan and Renaudie), 2 doctoral students, all at 100% time for 4 years; Dr. Lazarus (MfN: 50% time for ca 2 years), MfN provided lab tech Fr. Salzmann (75% for 4 years) plus assistance as needed from several other MfN staff scientists and technicians.

A detailed workplan is given as Appendix A. Briefly, Asatryan and one student will do the microfossil studies of WP2; Renaudie and a second student the geochemistry, modelling and syntheses of WP3 and 4; and Lazarus will lead the sample selection (WP1), assist both groups scientifically; plus act as senior advisor in project management, interaction with Museum administrators and external collaborators. We will have MfN/external support in geochemistry, biostratigraphy, taxonomy, ocean modelling, cluster computing and other areas. Hiring/training students, radiolarian/diatom taxonomy, sample selection and setting-up ocean modelling will occupy year 1; years 2 and 3 will be devoted to final age models, fossil data collection, testing and running full ocean simulations; and year 4 to project syntheses.

7. Feasibility and Risks

Our proposed study is fairly ambitious and will involve collecting a wide range of different proxy data for oceanographic and biodiversity change. We have been careful however to design a reasonable sampling and data collection strategy which is firmly founded on similar, successful projects in our own prior research, and which can be accomplished with our available manpower and time constraints. The majority of geologic sections have had at least preliminary studies for siliceous fossil content so inadequate preservation risks are, if not absent, low. Geologic age control is always a challenge but we have many sections available to us, and will use multiple stratigraphic age indicators (both siliceous and carbonate); thus we feel we will have adequate age control for the targeted resolutions of the study. While some of the methods are novel to this particular material, e.g. µCT, the method is well established in studies of geologically older radiolarians. Only the silicon isotopes can fairly be said to be risky, but we have included a wide array of other productivity proxies so we are not very dependent on any particular one. Ocean circulation simulations may not yield robust absolute global productivity estimates but should at least provide reasonable sensitivity analyses, which should be enough to illuminate the impact of of changing polar oceans and productivity on the system. We also point to the extensive resources available to us, including the MRC and other MfN collections, NSB database, our custom software for data collection and analyses, full lab facilities (with a brand-new lab expected ca end 2018), experienced lab technicians, plus our, and our collaborators, track records in these areas of research. Lastly, although the postdocs have several years research experience, neither have led such a complex study before. Management risk is however minimised by substantial involvement (50%, minimum) by a senior researcher (Lazarus) in the first half of the study (and unofficially also after his retirement in June 2020).

8. Broader implications

The proposed project is a unique blend of methods drawn from paleobiology/biodiversity, and paleoceanography/climate research, with the aim of providing an integrated understanding of a complex biologic-physical system. It will help build bridges between these two research communities, which should be communicating better with each other. The specific research design, lightly adapted, should be applicable to other time intervals and groups of fossils, providing a template for future integrated research of many important changes in the global earth-biology system over the Mesozoic and Cenozoic eras.

9. Dissemination of results

Primary scientific results will be published in ISI listed journals (as open access, publication fees in budget). We expect the key results will be suited to high ranked journals, while other results, e.g. new species descriptions, will go into normal specialty publications. Taxonomic information will also be published at the Mikrotax community online catalog as part of a new InterRad Society project (Lazarus, technical head). Microfossil occurrence data will be published via the MfN NSB Neptune database. Paleoceanographic data will be deposited in the Pangaea system; code at Github.

We also will take advantage of the MfN as host institution and develop an active program to communicate our research, and broader climate change issues to the public (which until now have not been very well developed in the Berlin museum landscape). These will be done within the framework of the MfN's normal outreach and educational activities and include exhibitions, citizen science activities, and internet based communication. Lastly, we will organise sessions at regular meetings, e.g. EGU, and will host a workshop for research specialists towards the end of year 3. This workshop will give us feedback to improve our own analyses in year 4, communicate our results to community members, and provide a starting point for planning future, post-project research.

10. Appendices

A - Time plan and list of workers (text and figure)
B - Budget (travel costs) - main budget directly submitted to website
C - CVs of principal investigators Asatryan, Renaudie, Lazarus
D - Statement of interests and motivation of Dr. Asatryan
E - Approval statements from MfN, Asatryan (for Lazarus as DAAD entry assistent)

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