Foraminifera in Extreme and Rapidly Changing Environments

FIERCE

Summary/Abstract The information contained in foraminifera shells is essential in understanding Earth's past climate system. Yet, most foraminiferal proxies (indicators of, for example, temperature, productivity, chemistry) and calibration efforts have focused on tropical-subtropical planktic species that live primarily in the sunlit ocean. FIERCE aims to provide a robust synthesis of research methods to improve our understanding of the biology and ecology of planktic foraminifera living in more extreme and rapidly changing environments such as oxygen minimum zones, the ice-ocean interface, high-latitude, and 'deeper' habitats (below the mixed layer). Without this, foraminiferal proxies in these environments are anecdotal, limiting past reconstructions and future climate change projections. Moving forward requires a multi-disciplinary, international effort, incorporating state-of-the-art research methods and input from across the ocean sciences. FIERCE WG members will test and fine-tune state-of-the-art research methods for studying FIERCE species at an international workshop in Peru and with WG members in the Norwegian Arctic. The resulting best practice 'standard operating procedures' (SOPs) for studying FIERCE species will be published in an open access, online platform. The SOPs will be broadly applicable to all planktic species and many benthic foraminifera, which expands the outcomes of this project well beyond FIERCE species. Furthermore, by focusing on foraminifera from understudied habitats, we will close a critical research gap and extend foraminifera utility in the fossil record beyond the ocean's sunlit mixed layer. Given the interdisciplinary and international nature of our vision, a SCOR working group is the best and most practical choice to achieve the proposed goals.

Scientific Background and Rationale

Planktic foraminifera are key contributors to global carbon cycling As major carbonate producers in the open ocean (Schiebel, 2002; Schiebel and Movellan, 2012), the production, flux to depth, and dissolution and burial of foraminiferal shells provides important feedbacks to the global carbon cycle (Grigoratou et al., 2021; Ridgwell and Zeebe, 2005). Their shells, preserved members of the pelagic ecosystem, have an extensive fossil record and serve as invaluable archives for climate proxies.

Planktic foraminifera with shallow (above pycnocline) depth habitats are well studied in comparison with FIERCE species. In fact, our knowledge about shallow tropical-subtropical planktic foraminifera has rapidly evolved (Bird et al., 2017; 2018; Dong et al., 2022;Takagi et

al., 2020). New techniques have led to a more in-depth understanding of specific diet, (previously identified by TEM and laboratory observations; see Schiebel and Hemleben, 2017, and references therein), bacterial interactions, and parasites in (Bird, et al., 2017; 2018; Greco et al., 2021). Other studies have found that shallow tropical planktic species host algal symbionts that pass on photosynthate to the host (Gast and Caron, 1996; Takagi et al., 2019; Lekieffre et al., 2018). FIERCE species may be symbiont-barren or facultative symbiont-bearing, although little is known about their preferred diet. Furthermore, understanding microbial interactions and predation is poorly understood in all planktic foraminifera species. This lack of understanding makes foraminiferal ecology difficult to model. As a result, foraminiferal turn-over and community shifts in the fossil record can be interpreted only in terms of environmental rather than ecological forcing, limiting and potentially skewing interpretations. Therefore a thorough understanding of all planktic foraminifera species ecology and physiology, including that of FIERCE species, is required to accurately model foraminiferal response to climate change in terms of biomass, habitat expansion/reduction and implications for the carbon cycling (Roy et al. 2015; Grigatorou et al. 2021).

Proxies are fundamental for extending marine instrumental records beyond the bounds of direct observation and for understanding long-term oceanographic and climate and environmental responses. Information about the upper ocean environments is recorded in the planktic foraminifera fossil shell/test, and expressed in their trace element and isotopic geochemistry (see Kucera et al., 2007; Katz et al., 2010). For shell geochemistry to function as a reliable proxy, well-defined relationships, or 'calibrations', between calcification environment and shell chemistry must be established, taking into account biological and ecological influences, such as calcification depth (Reynolds et al., 2018), microhabitat (Fehrenbacher et al., 2018), biomineralization processes, life cycle, diet, and symbiotic associations due to photosynthesis and respiration influence on shell geochemistry (Hönisch et al. 2003; Eggins et al. 2004). Biological or ecological offsets can often be accounted for using species-specific calibrations, (e.g. Bemis et al., 2002) but this has focussed on shallow (above the pycnocline) tropical-subtropical species, and not FIERCE species (Tierney et al., 2020; Gray and Evans, 2019; and references therein).

Contemporary global change disproportionately impacts extreme and rapidly changing environments such as tropical oxygen minimum zones (OMZ), the ice-ocean interface, and high-latitude regions which are warming at the most rapid rate on the planet (Serreze et al., 2009). OMZs are expanding (Breitburg et al., 2018; Keeling et al., 2010; Stramma et al., 2010; Schmidtko et al., 2017), oceans are becoming more acidic, sea ice is melting and salinity decreasing (Parkinson, 2019; Jones et al., 2020; Meier et al., 2021). Foraminiferal species that specifically live in these environments (FIERCE species) may provide records of biologically distinct environments (Hull et al., 2011; Dieckmann & Spindlery, 1991; Lu et al., 2016; Hoogakker et al., 2018; Greco et al., 2021; Davis et al., 2021; Winkelbauer et al., 2021). Significant attention has been given to studying the metabolic adaptations of benthic foraminifera in extreme environments (Risgaard-Petersen et al., 2006; Woehle et al., 2018; Orsi

et al., 2020; Gomaa et al., 2021). Yet, little is known about the biology and ecology of planktic FIERCE species. The consequence of this is that accurate foraminiferal proxy calibrations for these environments lag well behind those for more stable regions, and, critically, limit our understanding of the past conditions in these at-risk habitats. This gap in the proxy record also hinders a more holistic understanding of ocean processes, past, present and future. Therefore, reconstructing past changes, to underpin future projections for more 'extreme' environments has never been more needed.

Advances in ecology, geochemistry, genetics, modeling, and across the fields of biological and chemical oceanography make many of these key questions of FIERCE species' ecology and biology imminently answerable. By doing so, we can improve our ability to understand and reconstruct rapidly changing environments, connecting the past, present, and future of our oceans. However, accomplishing this goal will require a major transdisciplinary and international effort and an "un-siloing" of relevant methodologies from both within and outside of fields traditionally associated with foraminiferal research. By assembling a broad community base, explicitly codifying and openly disseminating relevant information, we can move forward in improving our understanding of FIERCE species and thus build new bridges between our understanding of past and future climate states.

Why a SCOR working group?

As foraminiferologists expand their scope into 'extreme' planktic environments, the assessment, articulation, and dissemination of the current state of knowledge, as well as the development of community standards, will become increasingly important. Our working group aims to produce a state-of-the-art synthesis of the ecology, biology, and geochemistry of planktic foraminifera from extreme environments, including an assessment of knowledge gaps. We will implement training early career and interdisciplinary scientists, featuring a developed route towards best practices and community standards, and, crucially, a forward-reaching plan to integrate foraminiferology with other marine sciences. The development of such a foundation will identify pressing research questions needed to expand the use of planktic foraminifera from "extreme" environments as oceanographic proxies. Furthermore, we aim to remove barriers to entry for early career and cross-disciplinary research by standardizing methods for research done across systems (model species, geography, and timescales) and make a crucial step towards knowledge transfer and sustainable capacity building during a training workshop and with the development of the SOPs. Moreover, developing a framework for cultivation, field collection, and preparation of living and fossil foraminifera from non-standard habitats will allow foraminiferal research to be more broadly integrated with efforts aimed at other zooplankton groups, and pelagic ecology more generally. Once general protocols and best-practice methodologies for extreme environments are developed, these can easily be expanded to other environments and ultimately guide long-term international projects that extend these protocols into a global sustainable ocean observation program. A SCOR working group is the best structure

to support these ambitious aims as they allow strong international and interdisciplinary collaborations to develop as well as a diverse network from which the SCOR WG can successfully disseminate SOPs to the broader community.

Terms of Reference

1. **Assess the current state of knowledge and identify critical gaps** (i.e., life history, genetics, ecology, biogeochemistry, preservation) in our understanding of living and fossil planktic foraminifera from 'extreme' environments. This assessment will draw from the varied expertise of full and associate working group members and be published as a review in an open-access journal.
2. **Create, validate, and publish an open-access portfolio of best practices** for the culturing, field-collection, and fossil preparation of foraminifera including those from 'extreme' environments. These best-practices include developing and testing a set of standard operating procedures (SOPs), detailed in the deliverables and made available in collaboration with GEOTRACES and the Ocean Best Practices System (OBPS).
3. **Develop open access training resources** for cross-disciplinary, early career and other scientists working with foraminifera from 'extreme' environments. Training resources will be grounded in and serve as a complement to written best practices documents. Resources will include video walk-throughs of field and laboratory procedures, slide decks, and recorded workshop sessions, aimed at researchers, students, and technicians.
4. **Develop a strategic plan for long-term international research and collaboration** in planktic foraminiferal research, planned with the input of a broad group of marine scientists, to more thoroughly integrate foraminiferal research with research in chemical and biological oceanography and marine ecology. This effort would culminate with a proposal for an international long-term project that promotes a sustainable global foraminifera observation and research. The addition of foraminifera observations supports the 'plankton diversity and distribution' Essential Ocean Variables of the Global Ocean Observation System (GOOS).

Working plan

WG members will develop and lead disciplinary groups (including biogeography, ecology, culturing, shell geochemistry, molecular biology) convened quarterly online and annually in person, in conjunction with international conferences, detailed below. Year one will focus on authoring a review of state-of-the-art practices and knowledge gaps (ToR1). This review forms the foundation for the SOPs, developed in year two, and the WG workshop at the start of year three. While SOPs are needed for all foraminiferal research, protocols will focus foraminifera from 'extreme' and understudied environments include methods for culturing non-spinose and asymbiotic species, protocols for collecting modern samples from deep (beyond the mixed layer) environments, and modified approaches for cleaning fragile shells.

To achieve ToR2 and parts of ToR3, FIERCE will hold a training workshop in Peru, develop a partnership with the Regional Research Graduate Network in Oceanography (RGNO) in Namibia, and provide training opportunities in the Arctic (see Capacity Building). The workshop in Peru will include prominent researchers across relevant fields who will apply and validate the state-of-the-art methods for research on foraminifera. The workshop location was selected in part to connect a growing center of foraminiferal research of the Biogeosciences Laboratory of the Universidad Peruana Cayetano Heredia with a broader international community. The facilities in Lima and Piura allow easy access to collect live and fossil foraminifera from diverse environments, including the Peruvian OMZ. During the two-week workshop FIERCE will test and iterate upon best practice protocols under development (ToR2), provide on-site training for workshop participants, and generate training resources (ToR3). This will include methods for live collection and culture, preservation of material for ecological, genetic, and geochemical analysis, and collection and preparation of fossil material for the same. FIERCE intends to partner with the SCOR endorsed Namibia RGNO, which allows access to the Namibia OMZ, where we will develop courses to complement existing training modules for the Benguela upwelling and Namibian OMZ. Furthermore, FIERCE will provide opportunities to join Arctic/Nordic (R/V Helmer Hanssen and R/V Kronprins Haakon) cruises to enable training in foraminifera ecology/culturing in extreme Arctic environments (cruise time in-kind contribution from members' home institution $20,000). During year two, we will also prepare tutorial videos and slideshows for SOPs that cannot be carried out on-site (e.g., SOPs for stable isotope and trace element analyses, electron and fluorescent microscopy imaging).

The SOPs developed from the workshops and off-site will be made available for training and public comment by submission to OBPS (ToR3). The review paper (ToR1) and subsequent SOP testing during the workshop and Arctic cruises will feed into online teaching resources (ToR2) and an online best practice manual (ToR2&3). Uniting transdisciplinary specialists through our international consortium and the creation of best practice methods protocols as well as identification of contemporary knowledge gaps will provide ample ideas to support the development of an international long-term research proposal(s) across years two to three (ToR4).

Timeline:

Year 1: The first FIERCE WG meeting will occur at FORAMS 2023 (Perugia, Italy), where we will plan our review paper, and assemble disciplinary subgroups leads (ToR1) for the identification of best practice protocols within their disciplines. Subgroup-meetings will be scheduled online every third month. We will also apply for funding to further support the organization and execution of the workshop (ship time, facility fees, accommodations) and travel (ECR Arctic cruises & Peru workshop). Potential funding agencies include (but not limited to) AGU, ASLO, GSA, EGU, the Micropalaeontological Society, Cushman Foundation, Twitter for Good, DFGD, NERC, Pages, NSF, NSF Taiwan, Lyell seed fund, JSPS, Chiba University.

Year 2: The second WG meeting will be held at the Ocean Sciences Meeting (New Orleans, USA), 2024. In conjunction with this meeting, we will convene a 1-day

transdisciplinary symposium, run by WG members, other plankton specialists, and interested conference attendees. The goal will be to discuss planktic foraminifera best practice protocols with leading scientists from adjacent research fields and share methods in foraminiferology with other relevant disciplines. By initiating this discussion at Ocean Sciences, we anticipate being able to convene a diverse group of marine scientists and connect early career scientists with an interdisciplinary community of marine scientists.

In parallel, subgroups would complete their disciplinary sections of the review article within the first 6 months, followed by another online full workgroup meeting during which combined versions of the review article and the best practice protocols will be discussed. The review article will be finalized and submitted (ToR1). Tutorial videos and slideshows for the best practice protocols will be created (ToR2) before the end of year 2.

Year 3: We will host a workshop in Piura and Lima, Peru (ToR2). The facilities at Piura provide a location to test protocols in a near-shore (shelf) environment less impacted by the OMZ, while the OMZ is extremely oxygen depleted close to Lima. The workshop would be split into two sessions, with the first focused on methods specific to living planktic foraminifera in Piura where we expect higher foraminifera abundances (WG member Cardich, personal communication). The second session would be held at the larger Lima facility, IMARPE, and will focus on both live and fossil collection methods involving foraminifera from low-oxygen environments.

The third WG meeting will be held in conjunction with the Peru workshops, where we will finalize best practices and training resources. Videos and slide decks from the training sessions will be edited and uploaded with the best practice portfolio in collaboration with GEOTRACES (ToR2&3). Participants and organizers can provide feedback after all resources are uploaded. We will also finalize the research proposal for a long-term project to sustain our SOPs and create the basis for a global ocean observation program in close collaboration with GOOS (ToR4). Funding agencies that will be targeted for our research proposal(s) include the European Research Council (synergy grants), the National Science Foundation (USA), the Natural Environmental Research Council (UK), and Research Council of Norway (Norway).

Deliverables

1. A **review paper** (ToR1) of the current state of knowledge of planktic foraminifera that live in low oxygen, deeper (beyond the mixed layer), and high-latitude environments will be published in an open-access peer reviewed journal. The paper will include information about depth habitat, life cycle, genotypes, preservation, and geochemistry, specifically targeting species from understudied habitats. Critical knowledge gaps will be identified with a list of key research areas required to bridge these gaps. Knowledge gaps will encompass uncertainties about extrapolation from shallow-dwellers, metabolism and adaptation to extreme environments, and symbioses and ecological interactions.

2. **Open access training resources** will include slide decks and filmed demonstrations of "**Standard Operating Procedures**" (SOPs) (see ToR 2&3, and Deliverable 3), and teaching resources for best-practices and protocols. Handling of foraminifera from both traditional and 'extreme' environments will be covered. We anticipate that learning modules we develop will be accessible online.
3. **Best practices for research** with cultured, field-collected, and fossil foraminifera will be detailed in comprehensive SOPs (ToR2&3). The SOPs would include instructions and photographs of methods for collecting live and dead plankton specimens from plankton tows, how to culture foraminifera, best practices for long term preservation of plankton tow collected specimens (formalin, ethanol) and sample preparation for analysis (e.g., geochemistry, genetics or microscopy).
4. **Preparation of a research proposal for an international long-term project** that extends the best practice sampling strategies and state-of-the-art methodologies into a global sustainable ocean observation program. (ToR4).

Capacity Building

The FIERCE working group aims to establish sustainable capacity building. One of the key limitations identified to moving the field of foraminiferal research forward is a disconnect between basic questions about the ecology, biology, and geochemistry of FIERCE species, and those with the toolkits to answer these questions. One rather straightforward example is that little is known about the lifecycle of deep dwelling planktic foraminifera - how long they live or what conditions may favor growth or reproduction. While geochemical methods may be readily transferable from better studied species, what environment or what timescale the geochemistry of deep-dwellers represents is unclear. To answer these questions will require tools from genetics, microbial ecology, and culture to be combined. By building capacity for diverse researchers to have open access to these tools, we anticipate this type and more complex questions may be more easily addressed.

In other cases, tools may be available but misunderstood or unstandardized. For example, the use of ethanol, which though widely used as a preservative in marine biological applications may alter the isotopic composition of foraminifera shells (Enge et al., 2018). This is a critical consideration when attempting to make biological to geochemical connections in foraminifera. Similarly, while the fluorescent calcein dye can be used to label laboratory-grown calcite, extended exposure may also alter the carbonate chemistry of the culture water, introducing a potential complication for foraminifera calcification (WG member Davis personal communication). While this information is informally "known" within some subfields, explicit codification is necessary to build capacity for broader collaboration. Codifying this type of knowledge within standard operating procedures would not only pave the way for greater collaboration and prevent wasted research effort, but can standardize approaches in ways that

make disparate collection and research efforts more compatible, such as has been done to great effect in GEOTRACES (see Cutter et al., 2017) or FOBIMO (foraminifera used for biomonitoring; see Schönfeld et al., 2012) programs.

We not only aim to build capacity by bringing in state-of-the-art skills and methodology to foraminiferal research but also to capacity build globally and generationally. We aim to codify standard practices within the field of foraminiferalogy and bring in tools from adjacent fields (e.g. genetics, geochemistry). Besides, the SOPs developed during this FIERCE project will also benefit researchers studying other plankton organisms (e.g. pteropods, copepods) and, more broadly, any marine research area using the same analytical techniques that will be covered by our set of "SOPs" (e.g. stable isotope analysis of other marine calcifiers).

In addition we plan to prepare a research proposal for an international long-term project that extends these best practice sampling strategies and state-of-the-art methodologies into a global sustainable ocean observation program.

These aims are highlighted in ToR3 and ToR4 and expanded on here. Specifically the FIERCE aims for capacity building include:

1. **Training early career scientists** in a range of techniques during our Peru workshop and Arctic cruise. Currently, state-of-the-art methodologies are infrequently applied to foraminifera, and this workshop will bring together researchers from wider disciplines to demonstrate the utility of new methods. These include for example the preparation and fixation of samples for molecular techniques, and the pre-cleaning used for trace element analyses for past environmental reconstructions including calcification temperatures. Slide decks and video tutorials will be made available online.
2. **Partner with the Namibia Research Discovery camps on Biogeochemical oceanography in Upwelling Ecosystems**. We will offer lectures (planktic foraminiferal communities of the EBUS system), lab work and training in sea-going sampling of foraminifera in the low oxygen environments off Namibia.
3. **Providing resources to scientists** by providing openly available best practices for working with cultured, field collected, and fossil foraminifera.
4. **Developing relationships between foraminiferologists and scientists in other disciplines**, including plankton ecology, microbiology, ecological and biogeochemical modeling to collaborate and co-supervise students to bring original cutting edge techniques into the field of foraminiferal studies.
5. **Identifying gaps in current knowledge**, many of which will require interdisciplinary & international partnerships and new approaches to fill. Those will be summarized in the planned overview (review-) paper.
6. **Building the foundation for extensive future sampling efforts** that meet the needs of the community and allow for integration with other related fields.

7. **Transferring knowledge about state-of-the-art methodologies to host facility** during the workshop in Peru: "hands-on" sessions and sustainability of these applications by capacity building at the host facility.
8. **Preparation of a proposal for a global sustainable ocean observation program** that sustains the developed best practice strategies. Our goal is to provide a blueprint for collecting foraminifera globally and expanding their utility in modern ocean research and in the paleorecord using internationally established protocols that guarantee results can be compared across studies and through time.

Working Group composition .

FIERCE WG has 10 Full and 10 Associate members that bring together state-of-the-art skills, including proxy development (species community, geochemical and morphometric analysis), molecular taxonomy, cell imaging, metabolic analysis, as well as field sampling, culturing, and experimental works, that will be fundamentals to achieve our ToRs. All Full members are working on foraminifera, however, they have diverse backgrounds and expertise from paleoceanography, genetics, protistology, and physiology, addressing a wide spectrum of research. The Associate members provide important input from the complementary fields covering biological oceanography, biodiversity modeling, functional modeling, and evolutionary biology. Our Full and Associate members represent 11 different nations/regions, including 2 emerging/developing nations (Peru and Brazil). Moreover, 7 of the Full members are female scientists, equally balanced as a whole in WG members. Half of our members are early career researchers, and they will be supported by experienced senior scientists including 2 Associate members who led SCOR WG138 (Darling, Tyszka), ensuring the success of organizing the WG.

Full Members (no more than 10, please identify chair(s))

Name	Gender	Place of work	Expertise relevant to proposal
1 Babette Hoogakker (Chair)	F	Heriot-Watt University (UK)	Foraminifera geochemistry, proxy development, paleoceanographic reconstructions (including seawater oxygen)
2 Catherine Davis (Chair) (early career)	F	North Carolina State University (USA)	Foraminiferal geochemistry, paleoceanography, live culture, foraminiferal ecology in low oxygen and low pH environments

3 Clare Bird (early career)	F	University of Stirling (UK)	Marine molecular microbiologist, foraminifera genotyping and single cell microbiome-barcoding
4 Jennifer Fehrenbacher	F	Oregon State University (USA)	Foraminifera geochemistry, proxy method development and paleoceanography, including high-latitude and deep dwelling species
5 Nicolaas Glock	M	University of Hamburg (GERMANY)	Foraminifera, biogeochemistry and nutrient budgets in low oxygen environments, metabolic rates, proxy development and paleoceanography
6 Charlotte LeKieffre (early career)	F	CNRS, CEA Grenoble (FRANCE)	Plankton cell structure and metabolism, electron microscopy and plankton symbiosis biology
7 Jorge Cardich (early career)	M	Universidad Peruana Cayetano Heredia, Lima (PERU)	Benthic foraminifera ecology in sediments in association with OMZs and coastal environments from Peru.
8 Abby Ren	F	National Taiwan University (TAIWAN)	Geochemistry and paleoceanography; Nitrogen isotopes in calcifiers, paleo-productivity, live culturing
9 Haruka Takagi (early career)	F	Chiba University (JAPAN)	planktic foraminifera ecology, symbiosis, photophysiology, global warming effects on foraminifera, symbiotic networks among microplankton
10 Rapheal Morard	M	MARUM (GERMANY)	Genetic and morphological diversity in Foraminifera Evolution of microplankton. Integration of genetic diversity in paleoceanography

Associate Member (no more than 10)

Name	Gender	Place of work	Expertise relevant to proposal
1 Kate Darling	F	University of Edinburgh/University of Stirling (UK)	Genetic diversity and biogeography of Foraminifera. Global evolutionary patterns of planktonic foraminifera
2 Julie Meilland (early career)	F	Marum (GERMANY)	Plankton sampling, planktonic foraminifera population dynamics and related C fluxes, high-latitude species culture
3 Christine Barras	F	LPG Angers (FRANCE)	Benthic foram culture, FOBIMO member (standardized protocol), foraminifera geochemistry, proxy development
4 Moriaki Yasuhara	M	The University of Hong Kong (HONG KONG)	Global biodiversity analyses
5 Hidetaka Nomaki	M	JAMSTEC (JAPAN)	(Benthic) culture, deep-sea sampling, biology of foram, analytical techniques (stable and radio isotopes, TEM, X-ray CT, NanoSIMS)
6 Mohamed M. Ezat (early career)	M	UiT the Arctic University of Norway (NORWAY)	Foraminifera geochemistry, proxy development and Arctic/high-latitude paleoceanography
7 Mattia Greco (early career)	M	IO PAN (POLAND)	Evolutionary biology, plankton ecology, bio-informatics, and phylogenetic analyses
8 Jaroslaw Tyszka	M	ING PAN (POLAND)	Modeling (eVolutus), fluorescent labeling and imaging
9 Douglas Villela de Oliveira Lessa (early career)	M	Federal Fluminense University (Niterói, Brazil) (BRAZIL)	Quaternary planktonic foraminifera taxonomy, (paleo)ecology, paleoceanography, statistics for simulating foram species distributions, transfer

			functions, stable isotopes and Mg/Ca proxies
10 Dimitri Gutiérrez	M	IMARPE (PERU)	Biological oceanography and paleoceanography. Director of research in oceanography and climate change at IMARPE

Working Group contributions

Babette Hoogakker is a paleoceanographer and works on the development and application of proxy methods to understand past ocean circulation and biogeochemical cycles. She has extensive experience in the proxy-reconstruction past seawater oxygen concentrations, using isotopic and trace metal measurements of foraminifera.

Catherine Davis has experience working with living, recent, and fossil foraminifera and is broadly interested in building bridges between modern- and paleo- oceanography. She uses tools from the individual shell (isotopic, trace element, and morphological analyses) to community (assemblage) level, with recent research focusing on how planktic foraminifera respond to and record low-oxygen and low-pH environments.

Clare Bird pioneers the use of molecular tools to understand foraminiferal metabolism, microbial interactions and adaptability to climate change. She has over ten years' experience in molecular microbiology and enjoys working at the interface between biology and (palae)oceanography.

Nicolaas Glock works at the interface between biogeochemistry, paleoceanography and micropaleontology and focuses on biogeochemical cycling in oxygen depleted marine environments. He studies metabolic and physiological adaptations of foraminifera to extreme environments, quantifies the role of foraminifera in marine nutrient cycling and uses foraminifera to reconstruct past nutrient cycling and redox conditions in oxygen depleted environments.

Jennifer Fehrenbacher has extensive experience culturing living planktic foraminifera and analyzing the isotopic and trace element geochemistry of modern and fossil shells. Her recent research focuses on understanding the geochemistry and ecology of deeper dwelling and higher latitude species in eastern boundary upwelling systems.

Charlotte LeKieffre research focuses on disentangling the functioning of protist cells involved in plankton symbiosis, especially the metabolic crosstalk between the symbionts and host cells. She has extensive experience with protist sampling and culturing, and stable isotope analysis, metabolomics, and electron microscopy.

Jorge Cardich studies the ecology of benthic foraminifera and other meiofaunal groups in relation to biogeochemical gradients of organic-rich and oxygen-poor marine environments, and

has promoted the studies of foraminiferal propagules from sediments of coastal environments from Peru. He has experience in the reconstruction of oxygenation in the past using microfossils and geochemical proxies.

Abby Ren researches the interaction between biology and the environmental conditions through the course of Earth history. She pioneers the work on developing planktonic foraminifera shell-bound nitrogen isotopes as a paleoceanographic tool to reconstruct past history of the marine nitrogen cycle and has extensive experiences working with foraminifera culturing, isotopic analyses on fossil and modern samples.

Haruka Takagi is broadly interested in modern planktic foraminifera species ecology and its interaction to the environment through geological time. Her current research focuses on understanding photosymbiosis in planktic foraminifera using stable isotope analysis, chlorophyll fluorescence, culture experiments and molecular biological techniques.

Raphael Morard works on genetics and morphological diversity of foraminifera. He is interested in the evolution of microplankton and integration of genetic diversity in paleoceanography.

Relationship to other international programs and SCOR Working groups:

The FIERCE working group will build upon and develop relationships with various international programs and existing SCOR working groups. For the development and publication of the SOPs we will work with GEOTRACES and OBPS. GEOTRACES (sponsored by SCOR) represents a well-established international research program that aims to improve the understanding of oceanic trace elements and isotopic biogeochemical cycles. It is an ideal partner to host globally accessible protocols designed to implement improved utility of foraminifera whose shells are recorders of the physico-chemical conditions of the ocean. We furthermore plan to base our SOPs on the GEOTRACES SOPs as well as the "Guide to Best Practices for Oceanic CO_2 Measurements", another SCOR sponsored effort. With GOOS we plan to define an observing system for planktic foraminifera by integrating them into the phytoplankton and zooplankton biomass and diversity Essential Ocean Variables.

Finally, we will collaborate with the "Biogeochemical Oceanography in Upwelling Ecosystems" organized by SCOR in Namibia. To this end, the Regional Research Graduate Network in Oceanography (RGNO) has expressed interest in proposing topics we could contribute to their program should this effort be funded. Members of our SCOR group are well poised to contribute to topics such as ocean acidification, planktic foraminifera communities, OMZs, and extending climate change records beyond the instrumental record based upon the needs of RGNO.

FIERCE benefits from outputs of the past SCOR WG138 "Modern Planktic Foraminifera and Ocean Changes," which focused on understanding tropical-subtropical species. The community has benefited from capacity building efforts and workshops hosted by WG138.

Beyond these direct connections, FIERCE science relates to several other SCOR WGs. MixONET is an active SCOR group with overlapping interests to those of FIERCE, in a desire to develop/improve biological oceanographic research methods to better apply to mixotrophs (foraminifera are non-constitutive mixoplankton); member Bird recently attended the MixITIN conference organized by MixONET. Additionally, there are common interests with MetaZooGene and EBUS. FIERCE will also be of interest to PAGES, especially the 2k-network (https://pastglobalchanges.org/science/wg/2k-network/intro) where our SOPs can inform calibration methods, and our focus on training for ECRs could be particularly relevant. FIERCE could also be of interest to mikrotax (https://www.mikrotax.org/pforams/), with increasing standardization in collecting both modern and fossil material bolstering taxonomic efforts. FIERCE workshops, outputs and progress will also be promoted through the Foraminifera Specialist Group of the Micropaleontological Society (member Hoogakker chair), and the Cushman Foundation. New links have also been developed with Protistology UK, a subgroup of the Microbiology Society, which is a multidisciplinary group utilizing and sharing diverse cutting edge molecular, culturing and biological methods to investigate diverse protists. These links will foster the development of new protocols for foraminifera.

Key References

Bemis, B. et al. (2002) *Mar. Micropal.* 46, 405-430.

Bird, C. et al. (2018) *PLoS One* 13, e0191653.

Bird, C. et al. (2017) *Biogeosciences* 14, 901-920.

Breitburg, D. et al. (2018) *Science* 359, 46.

Cutter G. et al. (2017) Sampling and Sample-handling Protocols for GEOTRACES Cruises, Version 3. *OceanBestPractices Repository.*

Davis, C.V. et al. (2021) *Biogeosciences* 18, 977–992.

Dieckmann, G.S. et al. (1991) *J. Foraminifer. Res.* 21. 182–189.

Dong, S. et al. (2022) *MDPI Biology* 11, 98.

Eggins, S.M. (2004) *Earth and Planet Sci. Lett.* 225, 411-419.

Enge, A.J. (2018) *Marine Micropaleontology* 144, 50-59

Gast, R. and Caron, D. (1996) *Molecular Biology and Evolution* 13, 1192–1197.

Gomaa, F. et al. (2021) *Sci. Adv.* 7: eabf1586.

Gray, W.R. and Evans, D. (2019) *Paleoceanogr. Paleoclimatol.* 34(3), 306-315.

Greco, M. et al. (2021) *J. Plankton Res.* 43, 113–125.

Grigoratou, M., et al. (2022). *Glob. Chan. Biol.* 28, 1063-1076.

Fehrenbacher, J.S., et al. (2018) *Geochim. et Cosmochim. Acta* 236, 361-372.

Hönish, B. et al. (2004) *Geochim. et Cosmochim. Acta* 68, 3675-3685.

Hoogakker, B.A.A. et al. (2018) *Nature* 562, 410-413.

Hull, P.M. et al. (2011) *Limnol. Oceanogr.* 56, 562–576.

Jones, M.C. et al. (2020) *Sci. Adv.* 6, eaaz9588.

Katz, M.E. et al. (2010) *J. Foraminifer. Res.* 40, 165–192.
Keeling, R.G., et al. (2010) *Annu. Rev. Mar. Sci*. 2, 199-229.
Kucera, M. (2007) *Mar. Geol.* 1, 213–262.
Lekieffre et al. (2018). *Scientific Reports*. 8:10140
Lu, Z. et al. (2016) *Nature Communications* 7, 11146.
Meier, W.N. et al. (2021) *NOAA Technical Report OAR Arctic Report Card*, 21-05.
Orsi, W.D. et al.. (2020) *ISME J.* 14, 2580–2594.
Parkinson, C.L. (2019) *PNAS* 16, 14414-14423.
Reynolds, C.E. et al. (2018) *Mar. Micropal.* 142, 92-104.
Ridgwell, A. and Zeebe, R.E. (2005) *Earth and Planet Sci. Letters* 234, 299-315.
Risgaard-Petersen, N. et al. (2006) *Nature* 443, 93–96.
Roy, T. et al. (2015) *Biogeoscience* 12, 2873, 2889.
Schiebel, R. (2002) *Global Biogeochem. Cy.* 16, 1065.
Schiebel, R. and Movellan, A. (2012) *Earth Syst. Sci. Data* 4, 75-89.
Schiebel, R. and Hemleben, C. (2017) *Planktic foraminifers in the Modern Ocean*. 358 pp
Schmidtko, S. et al. (2017) *Nature* 542, 335–339.
Schönfeld, J. (2012) *Marine Micropaleontology* 94–95: 1-13.
Serreze, M. C. et al. (2009) *Cryosphere* 3, 11–19.
Stramma, L., et al. (2010) *Deep-Sea Res. I* 57, 587-595.
Takagi, H. et al. (2019) *Biogeosciences* 16, 3377–3396.
Takagi, H. et al. (2020) *J. Plankton. Res.* 42, 403–410.
Tans, P.P. et al. (1979) *Nature* 280, 826–828.
Tierney, J.E. (2020) *Nature* 584, 569-573.
Winkelbauer, H. et al. (2021) *G-cubed* 22, e2021GC009811.
Woehle, C. et al. (2018) *Curr. Biol.* 28, 2536-2543.e5.

Appendix - Full Member Publications

Clare Bird

Bird, C., LeKieffre, C., Jauffrais, T., Meibom, A., Geslin, E., Filipsson, H.L., Maire, O., Russell, A.D. and Fehrenbacher, J.S. (2020) Heterotrophic foraminifera capable of inorganic nitrogen assimilation. *Frontiers in Microbiology*, 11:604979. https://doi.org/10.3389/fmicb.2020.604979

Bird, C., Schweizer, M., Roberts, A., Austin, W.E.N., Knudsen, K.L., Evans, K.M., Filipsson, H.L., Sayer, M.D.J., Geslin, E. and Darling, K.F. (2020). The genetic diversity, morphology, biogeography and taxonomic designations of *Ammonia* (Foraminifera) in the Northeast Atlantic. *Marine Micropaleontology*, 155:101726 https://doi.org/10.1016/j.marmicro.2019.02.001

Salonen, I.S., Chronopoulou, P-M., **Bird, C**., Reichart, G-J and Koho, K.A. (2019). Enrichment of intracellular sulphur cycle-associated bacteria in intertidal benthic foraminifera revealed by 16S and aprA gene analysis. *Scientific Reports*, 9:11692. https://doi.org/10.1038/s41598-019-48166-5

Bird, C., Darling, K.F., Russell, A.D., Davis, C.V., Fehrenbacher, J., Free, A., and Ngwenya, B.T. (2018). 16S rRNA gene metabarcoding and TEM reveals different ecological strategies within the genus *Neogloboquadrina* (planktonic foraminifer). *PLoS ONE*, 13(1): e0191653

Bird, C., Darling, K.F., Russell, A.D., Davis, C.V., Fehrenbacher, J., Free, A., Wyman, M., and Ngwenya, B.T. (2017). Cyanobacterial endobionts within a major marine planktonic calcifier (*Globigerina bulloides*, Foraminifera) revealed by 16S rRNA metabarcoding. *Biogeosciences*, 14(4), 901-920. DOI:10.5194/bg-14-901-2017

Jorge Cardich

Pitcher, G.C., Aguirre-Velarde, A., Breitburg, D., **Cardich, J.**, Carstensen, J., Conley, D.J., Dewitte, B., Engel, A., Espinoza-Morriberón, D., Flores, G., Garçon, V., Graco, M., Grégoire, M., Gutiérrez, D., Hernandez-Ayon, J.M., Huang, H.-H.M., Isensee, K., Jacinto, M.E., Levin, L., Lorenzo, A., Machu, E., Merma, L., Montes, I., SWA, N., Paulmier, A., Roman, M., Rose, K., Hood, R., Rabalais, N.N., Salvanes, A.G.V., Salvatteci, R., Sánchez, S., Sifeddine, A., Tall, A.W., Plas, A.K. van der, Yasuhara, M., Zhang, J., Zhu, Z.Y. (2021). System controls of coastal and open ocean oxygen depletion. *Progress in Oceanography* 197, 102613. https://doi.org/10.1016/j.pocean.2021.102613

Erdem, Z., Schönfeld, J., Rathburn, A.E., Pérez, M.E., **Cardich, J.**, Glock, N. (2020) Bottom-water deoxygenation at the Peruvian margin during the last deglaciation recorded by benthic foraminifera. *Biogeosciences*, 17, 3165–3182

Cardich, J., Sifeddine, A., Salvatteci, R., Romero, D., Briceño, FJ., Graco, M., Anculle, T., Almeida, C., Gutiérrez, D. (2019) Multidecadal changes in marine subsurface oxygenation off

central Peru during the last ca. 170 years. *Frontiers in Marine Science*, doi: 10.3389/fmars.2019.00270

Sommer, S., Gier, J., Treude, T., Lomnitz, U., Dengler, M., **Cardich, J.**, Dale, AW. (2016) Depletion of oxygen, nitrate and nitrite in the Peruvian oxygen minimum zone cause an imbalance of benthic nitrogen fluxes. *Deep-Sea Research I*, v. 112, p. 113-122.

Cardich, J., Gutiérrez, D., Romero, D., Pérez, A., Quipúzcoa, L., Morales, M., Marquina, R., Yupanqui, W., Solís, J., Carhuapoma, W., Sifeddine, A. (2015) Calcareous benthic foraminifera associated to geochemical conditions in the upper central Peruvian margin: control by pore water redox and sedimentary organic matter. *Marine Ecology Progress Series*, v. 535, p. 63-87, doi: 10.3354/meps11409.

Catherine Davis

Davis, C.V., Wishner, K., Renema, W. & P.M. Hull (2021) Vertical distribution of planktic foraminifera through an Oxygen Minimum Zone: how assemblages and shell morphology reflect oxygen concentrations. *Biogeosciences*, 18, 977–992, https://doi.org/10.5194/bg-18-977-2021, 2021.

Davis, C.V., Livsey, C.M., Palmer, H.M., Hull, P.M., Thomas, E., Hill, T.M., & C.R. Benitez-Nelson (2020) Extensive morphological variability in asexually produced planktic foraminifera. *Science Advances*, 6(28): abb8930, doi:10.1126/sciadv.abb8930.

Davis, C.V., Fehrenbacher, J.S., Benitez-Nelson, C., & R.C. Thunell (2020) Trace element heterogeneity across individual planktic foraminifera from the modern Cariaco Basin. *Journal of Foraminiferal Research*, 50(2): 204-218, doi:10.2113/gsjfr50.2.204.

Davis, C.V., Fehrenbacher, J.S., Hill, T.M., Russell, A.D. & H.J. Spero (2017) Relationships between temperature, pH, crusting and Mg/Ca in laboratory-grown *Neogloboquadrina* foraminifera. *Paleoceanography and Paleoclimatology*, 32(11): 1137-1152, doi:10.1002/2017pa003111.

Davis, C.V., Hill, T.M., Russell, A.D., Gaylord, B.P. & J. Jahncke (2016) Seasonality in planktic foraminifera of the Central California coastal upwelling region. *Biogeosciences,* 13: 5139-5150, doi:10.5194/bg-13-5139-2016.

Jennifer Fehrenbacher

Fritz-Endres, T., Dekens, P.S., **Fehrenbacher, J.S,** Spero, H.J., Stine, A.. (2019) Application of individual foraminifera Mg/Ca and $\delta^{18}O$ analyses for paleoceanographic reconstructions in active depositional environments, *Paleoceanography and Paleoclimatology*, 34(10), 1610-1624.

Reynolds, C.E., Richey, J.N, **Fehrenbacher, J.S.,** Rosenheim, B.E., Spero, H.J.. (2018) Environmental controls on the geochemistry of *Globorotalia truncatulinoides* in the Gulf of

Mexico: Implications for paleoceanographic reconstructions, *Marine Micropaleontology*, 142, 92-104.

Fehrenbacher, J.S., Russell, A.D., Davis, C.V., Spero, H.J., Chu, E., Hönisch, B. (2018) Ba/Ca ratios in the non-spinose planktic foraminifer *Neogloboquadrina dutertrei*: Evidence for an organic aggregate microhabitat. *Geochimica et Cosmochimica Acta*, 236, 361-372.

Fehrenbacher, J.S., Russell, A.D., Davis, C.V., Gagnon, A.C., Spero, H.J., Cliff, J.B., Zhu, Z., Martin, P. (2017) Link between light-triggered Mg-banding and chamber formation in the planktic foraminifera *Neogloboquadrina dutertrei*, *Nature communications*, 8, 15441.

Gibson, K.A., Thunell, R.C., Machain-Castillo, M.L., **Fehrenbacher, J.S**., Spero, H.J., Wejnert, K.,Nava-Fernández, X., Tappa, E.J. (2016) Evaluating controls on planktonic foraminiferal geochemistry in the Eastern Tropical North Pacific, *Earth and Planetary Science Letters*, Vol. 452, 90-103.

Nicolaas Glock

Glock, N., Romero, D., Roy, A.-S., Wöhle, C., Dale, A.W., Schönfeld, J., Wein, T., Weissenbach, J., Dagan, T. (2020) A hidden sedimentary phosphate pool inside benthic foraminifera from the Peruvian upwelling region might nucleate phosphogenesis. *Geochimica et Cosmochimica Acta*, 289, 14-23.

Glock, N., Roy, A.-S., Romero, D., Wein, T., Weissenbach, J., Revsbech, N.-P., Høgslund, S., Clemens, D., Sommer, S., Dagan, T. (2019) Metabolic preference of nitrate over oxygen as electron acceptor in Foraminifera from the Peruvian oxygen minimum. *PNAS*, 116 (8) 2860-2865. doi/10.1073/pnas.1813887116.

Glock, N., Erdem, Z., Wallmann, K., Somes, C., Liebetrau, V., Schönfeld, J., Gorb, S., Eisenhauer, A. (2018) Coupling of oceanic carbon and nitrogen facilitates spatially resolved quantitative reconstruction of nitrate inventories. *Nature Communications*, 9, 1217.

Wöhle, C., Roy, A.-S., **Glock, N.,** Wein, T., Weissenbach, Rosenstiel, P., Hiebenthal, C., Michels, J., Schönfeld, J., Dagan, T. (2018) A novel eukaryotic denitrification pathway in foraminifera. *Current Biology*, 28, 2536-2543.

Glock, N., Schönfeld, J., Eisenhauer, A., Hensen, C., Mallon, J., Sommer, S. (2013). The role of benthic foraminifera in the benthic nitrogen cycle of the Peruvian oxygen minimum zone. *Biogeosciences*, 10, 4767-4783.

Babette Hoogakker

Hoogakker, B.A.A., Anderson, C., Paoloni, T., Stott, A., Grant, H., Keenan, P., Mahaffey, C., Blackbird, S., McClymont, E., Rickaby, R., Poulton, A., Peck, V. (in review). Planktonic

foraminifera organic carbon isotopes as novel archives of upper ocean carbon cycling. *Nature Communications*.

Reyes-Macay, D., **Hoogakker, B.**, Martinez-Mendez, G., Llanillo, P.J., Grasse, P., Mohtadi, M., Mix, A., Leng, M.J., Struck, U., McCorkle, D.C., Troncoso, M., Gayo, E.M., Lange, C.B., Farias, L., Carhuapoma, W., Graco, M., Cornejo-D'Ottone, M., De Pol Holz, R., Fernandez, C., Narvaez, D., Vargas, C.A., Garcia-Araya, F., Hebbeln, D. (2022) Isotopic characterization of water masses in the Southeast Pacific region: paleoceanographic implications. *Journal of Geophysical Research: Ocean,* 129 , 1, e2021JC017525.

Winkelbauer, H., Cordova-Rodriguez, K., Reyes-Macaya, D., Scott, J., Glock, N., Lu, Z., Hamilton, E., Chenery, S., Holdship, P., Dormon, C., **Hoogakker, B.** (2021) Foraminifera iodine to calcium ratios: approach and cleaning. *Geochemistry, Geophysics, Geosystems,* 22(11), e2021GC009811.

Lear, C.H., Anand, P., Blenkinsop, T., Foster, G.L., Gagen, M., **Hoogakker, B**., Larter, R.D., Lunt, D.J., McCave, I.N., McClymont, E., Pancost, R.D., Rickaby R.E.M., Schultz, D.M., Summerhayes, C.J.R., Zalasiewics, J. (2021). Geological society of London scientific statement: What the geological record tells us about our present and future. *Journal of the Geological Society,* 178.

Hoogakker, B.A.A., Lu, Z., Umling, N., Jones, L., Zhou, X., Rickaby, R.E.M., Thunell, R., Cartapanis, O., Galbraith, E. (2018). Glacial expansion of oxygen-depleted water in the eastern tropical Pacific. *Nature* 562, 410-413.

Charlotte LeKieffre

Decelle J., Veronesi G., **LeKieffre C.**, Gallet B., Chevalier F., Stryhanyuk H., Marro S., Ravanel S., Tucoulou R., Schieber N., Finazzi G., Schwab Y. and Musat N. (2021) Subcellular architecture and metabolic connection in the planktonic photosymbiosis between Collodaria (radiolarians) and their microalgae. *Environmental Microbiology*, 23: 6569-6586. https://doi.org/10.1111/1462-2920.15766

LeKieffre C., Spero H.J., Fehrenbacher J.S., Russell, A.D., Ren H., Geslin E. and Meibom A. (2020) Ammonium is the preferred source of nitrogen for planktonic foraminifer and their dinoflagellate symbionts. *Proceedings of the Royal Society B*. 287: 20200620. http://doi.org/10.1098/rspb.2020.0620

LeKieffre C., Bernhard J. M., Mabilleau G., Filipsson H.L., Meibom A., Geslin E. (2018). An overview of cellular ultrastructure in benthic foraminifera: New observations of rotalid species in the context of existing literature. *Marine Micropaleontology*, 138: 12-32. https://doi.org/10.1016/j.marmicro.2017.10.005

LeKieffre C., Spero H.J., Russell A.D. Fehrenbacher J.S., Geslin E. and Meibom A. (2018) Assimilation, translocation, and utilization of carbon between photosynthetic symbiotic dinoflagellates and their planktic foraminifera host. *Marine Biology* 165**,** 104. https://doi.org/10.1007/s00227-018-3362-7

LeKieffre C., Spangenberg J. E., Mabilleau G., Escrig S., Meibom A., Geslin E. (2017) Surviving anoxia in marine sediments: The metabolic response of ubiquitous benthic foraminifera (*Ammonia tepida*). *PLoS ONE* 12(5): e0177604. https://doi.org/10.1371/journal.pone.0177604

Raphael Morard

Cordier, T., Angeles, I.B., Henry, N., Lejzerowicz, F., Berney, C., **Morard, R**., Brandt, A., Cambon-Bonavita, M.-A., Guidi, L., Lombard, F., Arbizu, P.M., Massana, R., Orejas, C., Poulain, J., Smith, C.R., Wincker, P., Arnaud-Haond, S., Gooday, A.J., de Vargas, C., Pawlowski, J. (2022) Patterns of eukaryotic diversity from the surface to the deep-ocean sediment. *Sci. Adv.,* 8, 26–28. doi:10.1126/sciadv.abj9309

Morard, R., Vollmar, N.M., Greco, M., Kucera, M. (2019) Unassigned diversity of planktonic foraminifera from environmental sequencing revealed as known but neglected species. PLoS One 14, e0213936. doi:10.1371/journal.pone.0213936

Morard, R., Mahé, F., Romac, S., Poulain, J., Kucera, M., de Vargas, C. (2018) Surface ocean metabarcoding confirms limited diversity in planktonic foraminifera but reveals unknown hyper-abundant lineages. *Scientific reports*, 8:2539, 1–10. doi:10.1038/s41598-018-20833-z

de Vargas, C., Audic, S., Henry, N., Decelle, J., Mahe, F., Logares, R., Lara, E., Berney, C., Le Bescot, N., Probert, I., Carmichael, M., Poulain, J., Romac, S., Colin, S., Aury, J.-M., Bittner, L., Chaffron, S., Dunthorn, M., Engelen, S., Flegontova, O., Guidi, L., Horak, A., Jaillon, O., Lima-Mendez, G., Luke, J., Malviya, S., **Morard, R**., Mulot, M., Scalco, E., Siano, R., Vincent, F., Zingone, A., Dimier, C., Picheral, M., Searson, S., Kandels-Lewis, S., Acinas, S.G., Bork, P., Bowler, C., Gorsky, G., Grimsley, N., Hingamp, P., Iudicone, D., Not, F., Ogata, H., Pesant, S., Raes, J., Sieracki, M.E., Speich, S., Stemmann, L., Sunagawa, S., Weissenbach, J., Wincker, P., Karsenti, E., Boss, E., Follows, M., Karp-Boss, L., Krzic, U., Reynaud, E.G., Sardet, C., Sullivan, M.B., Velayoudon, D. (2015) Eukaryotic plankton diversity in the sunlit ocean. *Science* (80-.), 348, 1261605–1261605. doi:10.1126/science.1261605

Morard, R., Darling, K.F., Mahé, F., Audic, S., Ujiié, Y., Weiner, A.K.M., André, A., Seears, H. a., Wade, C.M., Quillévéré, F., Douady, C.J., Escarguel, G., de Garidel-Thoron, T., Siccha, M., Kucera, M., de Vargas, C. (2015) PFR^2 : a curated database of planktonic foraminifera 18S ribosomal DNA as a resource for studies of plankton ecology, biogeography and evolution. *Mol. Ecol. Resour*. 15, 1472–1485. doi:10.1111/1755-0998.12410

Haojia Abby Ren

Smart, S.M., Fawcett, S.E., **Ren, H.**, Schiebel, R., Tompkins, E.M., Martínez-García, A., Stirnimann, L., Roychoudhury, A., Haug, G.H., Sigman, D.M. (2020) The nitrogen isotopic composition of tissue and shell-bound organic matter of planktic foraminifera in Southern Ocean surface waters. *Geochemistry, Geophysics, Geosystems*, 21, e2019GC008440. https://doi.org/10.1029/2019GC008440.

Smart, S.M., **Ren, H.,** Fawcett, S.E., Schiebel, R., Conte, M., Rafter, P.A., Ellis, K.K., Weigand, M.A., Oleynik, S., Haug, G.H., Sigman D.M. (2018) Ground-truthing the planktic foraminifer-bound nitrogen isotope paleo-proxy in the Sargasso Sea, *Geochimica et Cosmochimica Acta*, 235, 463-482. doi:10.1016/j.gca.2018.05.023.

Schiebel, R., Smart, S.M., Jentzen, A., Jonkers, L., Morard, R., Meilland, J., Michel, E., Coxall, H.K., Hull, P.M., de Garidel-Thoron, T., Aze, T., Quillévéré, F., **Ren, H.**, Sigman D.M., Vonhof, H.B., Martínez-García, A., Kučera, M., Bijma, J., Spero, H.J., Haug, G.H. (2018) Advances in planktonic foraminifer research: New perspectives for paleoceanography, *Revue de Micropaléontologie*, 61, 3–4, 113-138, ISSN 0035-1598.

Ren, H., Studer, A.S., Serno, S. Sigman D.M., Winckler, G., Anderson, R.F., Oleynik, S., Gersonde, R., Haug, G.H. (2015) Glacial-to-interglacial changes in nitrate supply and consumption in the subarctic North Pacific from microfossil-bound N isotopes at two trophic levels, *Paleoceanography*, 30, 1217–1232.

Ren, H., Sigman D.M., Thunell, R.C., Prokopenko, M.G. (2012) Nitrogen isotopic composition of planktonic foraminifera from the modern ocean and recent sediments, *Limnology and Oceanography*, 57(4), 1011-1024.

Haruka Takagi

Takagi, H., Kimoto, K., Fujiki, T. (2022) Photosynthetic carbon assimilation and electron transport rates in two symbiont-bearing planktonic foraminifera. *Frontiers in Marine Science*, 9, 803354

Takagi, H., Kurasawa, A., Kimoto, K. (2020) Observation of asexual reproduction with symbiont transmission in planktonic foraminifera. *Journal of Plankton Research*, 42, 403–410.

Takagi, H., Kimoto, K., Fujiki, T., Saito, H., Schmidt, C., Kucera, M., Moriya, K. (2019) Characterizing photosymbiosis in modern planktonic foraminifera. *Biogeosciences*, 16, 3377–3396.

Takagi, H., Kimoto, K., Fujiki, T., Moriya, K. (2018) Effect of nutritional condition on photosymbiotic consortium of cultured *Globigerinoides sacculifer* (Rhizaria, Foraminifera). *Symbiosis*, 76, 1–15.

Takagi, H., Moriya, K., Ishimura, T., Suzuki, A., Kawahata, H., and Hirano, H. (2016) Individual migration pathways of modern planktic foraminifers: Chamber-by-chamber assessment of stable isotopes. *Paleontological Research*, 20, 268–284.