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PREFACE

The IceAGE project – a follow up of BIOICE

Icelandic marine Animals: Genetics and Ecology

The Nordic Seas, *i.e.* the Greenland, Iceland and Norwegian Seas (GIN Seas), and the northernmost part of the North Atlantic Ocean, are characterized by several local peculiarities like submarine ridges (geographical barriers) and influence of water masses of different origin. The large Greenland-Iceland-Faeroe submarine ridge (GIF Ridge) has its deepest saddle depth of 840 m in the Faeroe Channel (Fig. 1) and separates the deep Arctic and Nordic Seas from the deep North Atlantic Ocean. Accordingly, the ecological conditions are different between these regions, and there is a sharp temperature gradient across the ridge. Because of these geological and oceanographic characteristics, the marine environment around Iceland is the confluence of three very different marine environments, namely the boreal, subarctic and Arctic zones. The resultant intersection of these zones provides interesting possibilities for biological research. More specifically, the confluence of ridge systems and oceanographic water masses around Iceland allows an unprecedented opportunity to assess how ecology and evolution are shaped by physical characteristics in marine systems.

Knowledge of benthic organisms in Icelandic waters stems from the remarkable Danish *Ingolf* expedition (Wandel 1899) which explored waters around the Faeroe Islands, Iceland and Greenland during four months each year in 1895 and 1896. This effort was the first large-scale, scientific, benthic exploration in the region. During these expeditions a fine mesh was for the first time used in the sampling gear to separate the smaller benthic invertebrates from the sediments, leading to discovery of many small, unknown isopod, tanaidacean and cumacean species (see Hansen 1913, 1916, 1920). Outcomes from these expeditions included large monographs on various invertebrates in the series *The Danish Ingolf*

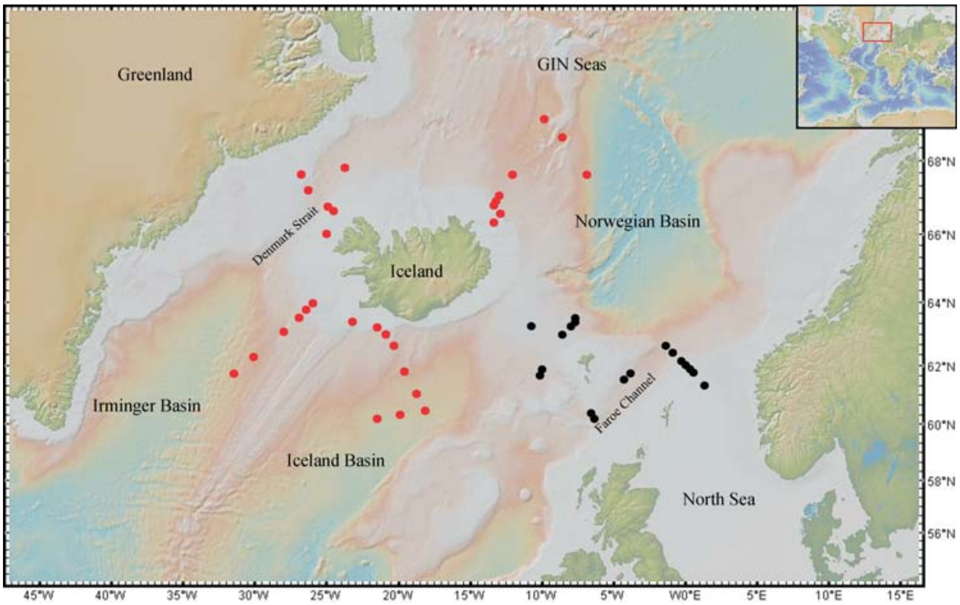

Fig. 1. Map of the sampling area. Red dots indicating IceAGE1 (M85/3), black dots indicating IceAGE2 (POS456).

Expedition. This was later followed by the *Zoology of Iceland* series (Friđriksson and Tuxen 1937 onwards; Madsen 1949), which surveyed fauna of Iceland and Icelandic waters to the limits of the continental shelf. Although this series included terrestrial and fresh water forms, most volumes dealing with the marine systems were published between 1937 and 1952 (*e.g.* Stephensen 1937, 1940; Kramp 1938; Thorson 1941; Wesenberg-Lund 1951), with sporadic volumes after that. The last on the marine environment dealt with the intertidal communities (Ingólfsson 2006).

The very successful BIOFAR project (*Biology of the Faeroe Islands*) was initiated by Norwegian and Danish marine biologists (Nørrevang *et al*. 1994) and sampled approximately 600 localities in Faeroese waters. BIOFAR lead to extensive new knowledge on benthic invertebrates in the region (*e.g.* Schander 1995; Sneli *et al*. 2005). Based on BIOFAR, from 1992 to 2004, the international BIOICE project (*Benthic Invertebrates of ICElandic waters*) has focused on the collection and characterization of benthic invertebrates within the Icelandic economic zone. Many of the scientists involved in BIOFAR helped realizing the BIOICE project. Data from the BIOICE project has greatly expanded our knowledge of the benthic invertebrates in this region, their taxonomy, distribution and diversity (*e.g.* Bird and Holdich 1989; Svavarsson 1997; Weisshappel and Svavarsson 1998; Schuchert 2000, 2001; Weisshappel 2000, 2001; Sigvaldadóttir 2002; Parapar 2003, 2006; Bird 2004a,b; Stransky and Svavarsson 2006; Brix and Svavarsson 2010;

Fig. 2. Group picture of scientists on board of R/V *Meteor* during IceAGE1 (M85/3). From left to right, row 1: Sigrún Haraldsdóttir, Magda Błażewicz-Paszkowycz, Johanna Cannon, Saskia Brix, Nina Mikkelsen, Wiebke Bauernfeind, Alexandra Ostmann, Sahar Khodami; row 2: Sven Hoffmann, Pedro Martinez, Karin Meißner, Anna Murray, Yolanda Lucas Rodriguez, Karen Jeskulke, Sabine Holst, Moriaki Yasuhara; 3. row: Dario Fiorentino, Kevin Kocot, Dieter Fiege, Nils Brenke, Sarah Schnurr, Rob Jennings, Guillermo Diaz Agras, Hermann Neumann, Torben Riehl, Jörundur Svavarsson (Valeska Borges not on the picture). Picture taken by Captain Michael Schneider.

Fig. 3. Group picture of scientists on board of R/V *Poseidon* during IceAGE2 (POS456). From left to right: Johanna Cannon, Jörundur Svavarsson, Mari Eilertsen, Matthes Kenning, Sarah Schnurr, Rob Jennings, Saskia Brix, Sven Hoffmann, Pedro Martinez, Karen Jeskulke, Sabine Holst. Picture taken by Captain Klaus Ricke.

Moreira and Parapar 2012; Dauvin *et al*. 2012; Parapar *et al*. 2012; Meißner *et al*. 2014; Schnurr *et al*. 2014). The BIOICE project has also benefitted ecological knowledge (*e.g*. Guđmundsson *et al*. 2000; Ólafsdóttir and Svavarsson 2002; Guđmundsson *et al*. 2003; Brökeland *et al*. 2010). In short, the shallow water fauna around Iceland is much more similar to the fauna of the North-east Atlantic than to the fauna of the West Atlantic. A low diversity in the arctic deep-sea fauna has for a long time been recognized (*e.g*. Stephensen 1940; Bouchet and Warén 1979; Sibuet 1979; Svavarsson *et al*. 1993).

Despite the extensive effort in BIOICE (19 cruises, samples from 1412 localities) there is still much to be learned about the benthic organisms in the region. The area is large (>750 000 km^2) and deep waters in the Iceland and Irminger Basins and the GIN Seas are still undersampled. Earlier evaluations (*e.g*. Stephensen 1940; Wesenberg-Lund 1951; and other contributions from *Zoology of Iceland*) were, however, mainly based on data collected in shallow waters, some deep water samples originating from the Danish *Ingolf* expedition. Additionally, molecular studies (*i.e*. phylogeography, phylogeny) of Icelandic marine invertebrates are scarce (except some intertidal or shallow water studies, *e.g*. Handschumacher *et al*. 2010; Krebes *et al*. 2011). Such studies are crucial for understanding cryptic or unrecognized biodiversity and the evolutionary history of the region.

Due to increasing temperatures, the region may be subject to extensive changes that influence benthic organisms. Changes in organismal distributions, community structure and diversity are concerns in the coming years given Iceland's location in a climatically sensitive area. Studies suggest that the complex hydrography (Hansen and Østerhus 2000) has a high sensitivity to climate change scenarios. An inventory of the fauna, including its genetics (phylogeography, phylogeny) and ecology, sets a baseline for later reference and is of major importance for a better understanding of how marine environments respond to climate change. Additionally, factors influencing distribution and migration of species need to be addressed. Such questions are focused on in the IceAGE (*Icelandic marine Animals – Genetics and Ecology*) project. This project was developed during several meetings in Germany and Iceland to facilitate analyses integrating classical taxonomy, molecular tools and ecological modelling. The IceAGE project is aimed to develop into a long-term study. So far, two international research cruises have been undertaken, IceAGE1 (M85/3, Fig. 2) with R/V *Meteor* and IceAGE2 (POS456, Fig. 3) with R/V *Poseidon* in August 2013 (http://www.ifm.zmaw.de/fileadmin/files/leitstelle/meteor/M85/M85-3-SCR.pdf; http://www.geomar.de/fileadmin/content/zentrum/ze/fs/Poseidon_Berichte_2013_PDF/POS456_Brix.pdf). Both expeditions were highly successful, resulting in sampling of the benthic fauna at 31 working areas (267 stations, each gear deployment defined as "station" within the larger area) during IceAGE1 and 17 areas (86 stations) during IceAGE2 at depths between 117 and 2780 m (see Fig. 1). Each dot in the figure represents a working area, being a 2–5 nautical miles circle where a standardized set of gear (CTD, multicorer, boxcorer, epibenthic sled and trawl or triangle dredge) was deployed. The CTD was always deployed first, setting the central point of the circle (Fig. 4). All benthic sampling devices were deployed around this point in order to have the abiotic data available for all samples. Whenever time and weather conditions allowed replicate sampling, replicates were taken by boxcorer and epibenthic sled. We used two types of epibenthic sleds (Rothlisberg and Pearcy 1977; Brenke 2005; Brandt *et al.* 2013), the latest version equipped with a camera system (Brandt *et al.* 2013).

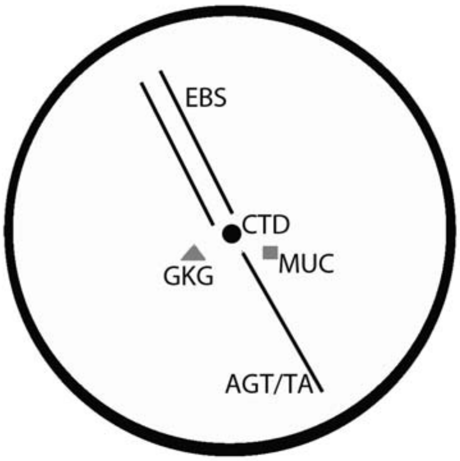

Fig. 4. Sampling design. Schematic view of a working area defined as 2–5 nautical mile circle with gear deployments around the central CTD measurement.

Sorting of the IceAGE1 samples took place at the *Sandgerđi Marine Centre* and the *University of Iceland* (Iceland) and the *German Centre for marine Biodiversity Research* (DZMB) in Germany as a joint effort. Samples are available on request from Iceland (contact: Jörundur Svavarsson) and Germany (contact: Saskia Brix, Karin Meißner & Pedro Martinez Arbizu). For IceAGE2, all benthic samples are sorted at the DZMB. We anticipate that sorting of IceAGE samples will be completed in 2016. Samples are housed in the *Meteor* archives (http://www.material-archiv.de/en/home.html) and can be made available to interested individuals at any time.

Preserving samples for molecular work during IceAGE was an important aspect of the project's sampling design (Riehl *et al*. this issue). The "cooling chain" is extremely important to ensure rapid and thorough preservation of specimens of all types. Specimens were kept cold from the time when live samples were collected from the bottom of the ocean, fixed in cold 96% undenatured ethanol (EtOH), sorted on ice, and finally stored at 0–4°C after sorting. The use of formaldehyde to preserve the vast majority of the specimens collected during the BIOICE cruises precludes most of these specimens for molecular work (but see

Schander and Halanych 2003; Skage and Schander 2007). In contrast, during the IceAGE cruises samples were preserved for both, molecular and morphological research. For example, samples from the RP epibenthic sled (Rothlisberg and Pearcy 1977) were decanted onto sieves and separated into fractions; the smallest fraction (300 µm) was preserved in ethanol, while the larger two (500 µm and 1000 µm) could have a subsample removed for immediate cold-sorting followed by ethanol preservation, with the remainder preserved in formalin. Sorting of ethanol-preserved material at the DZMB and of formalin-preserved material at Sandgerđi made use of each group's expertise. Some fraction of IceAGE samples from all gear were preserved for DNA-based studies using 96% undenatured ethanol with the "cooling chain" described above. Additionally, tissue samples from especially rare or otherwise significant specimens were preserved for RNA-based studies such as transcriptome sequencing (Todt and Kocot this issue) and in *situ* hybridization. Because of the careful treatment applied to samples collected during the IceAGE cruises, most specimens should also be suitable for whole genome sequencing applications.

The present IceAGE special issue presents first results of the IceAGE project. The habitats sampled during IceAGE cruises are described by Meißner *et al*. based on video and image analyses as well as information on sediments and hydrography (cross reference Meißner *et al*. this issue). Furthermore, the abiotic factors are presented for all areas (Ostmann *et al*. this issue). Moriaki Yasuhara and colleagues (Yasuhara *et al*. this issue) report on deep-sea ostracod assemblages sampled during IceAGE1 using the multicore (MUC) and epibenthic sled (EBS). Their results show distinct shelf and lower-bathyal faunas, and the importance of using multiple sampling gears (as done in IceAGE) in order to get a clearer picture of benthic microinvertebrate biodiversity. Julio Parapar and colleagues (Parapar *et al*. this issue) examine Icelandic Ampharetidae, an ecologically important group of benthic polychaetous annelids, and report on their geographic and depth distribution as well as microscopic anatomy using scanning electron microscopy (SEM). Sarah Schnurr and Marina Malyutina (Schnurr and Malyutina this issue) describe two new species of munnopsid isopods (Asellota) from the genus *Eurycope*, thus further expanding the known diversity of this already diverse clade in Icelandic waters. Brix *et al.* (this issue) detect underestimated diversity inside the isopod species *Chelator insignis*. Also contributing to the known diversity of Icelandic invertebrates, Nina Mikkelsen and Christiane Todt (Mikkelsen and Todt this issue) describe a new species of aplacophoran mollusc belonging to Caudofoveata. Further, they report on the distribution of the seven species of caudofoveates sampled around Iceland and report the first record of another species, *Falcidens halanychi*, in Icelandic waters. Also working on aplacophoran molluscs, Christiane Todt and Kevin Kocot (Todt and Kocot this issue) describe a new species of Solenogastres that has the unusual habit of brooding its eggs in its mantle cavity. This work expands our knowledge of the diversity of Icelandic aplacophorans and provides new insight into the reproductive biology of these unusual molluscs. Magda Błażewicz-Paszkwycz and co-authors use molecular methods to identify sexually dimorphic tanaidaceans to species, and provide some of the first morphological descriptions of fully identified swimming males (Błażewicz-Paszkowycz *et al*. this issue). Piotr Jóźwiak describes a new genus of mostly Icelandic Tanaidacea as part of an ongoing effort to revise the taxonomy of this diverse crustacean clade (Jóźwiak this issue). Rob Jennings and Ron Etter analyze population genetic diversity of Icelandic populations of the deep-sea protobranch bivalve *Nucula atacellana,* describing the potential for long-distance connectivity across the North Atlantic, restricted connectivity with GIN seas, and pathways of pan-Atlantic colonization and expansion for this species (Jennings and Etter this issue).

Fig. 5. Professor Dr. Christoffer Schander (1960–2012).

The issue is dedicated to Christoffer Schander (1960–2012), University of Bergen and University Museum of Bergen, who was involved in the planning of the IceAGE project (Fig. 5). His contribution to organismal knowledge of the region was extensive. Christoffer specialized in molluscs with his primary areas of expertise being the extremely diverse, parasitic pyramidellid gastropods and the worm-like aplacophorans. Nonetheless, he was broadly interested in benthic invertebrates of all types and biodiversity patterns. He was very active in promoting studies of biodiversity in the Northern Atlantic. Importantly, he enthusiastically and avidly supported other scientists with his time and knowledge and was especially supportive of students. He passed away 20th February 2012, at the age of just 52. He is sorely missed by his colleagues and friends.

Initiated as outcome of the *IceAGE workshop 4: Genetic Results* held September in 2012 in Wilhelmshaven (Germany) financed by the German Science Foundation under contract No. BR3843/5-1, we wish to thank the Committee on Polar Research, Polish Academy of Sciences, for inviting us to have this special issue in *Polish Polar Research* and in particular Magda Błażewicz-Paszkowycz for her enthusiasm and effort in making this issue a reality. Pedro Martinez Arbizu greatly encouraged us to develop the IceAGE project and without his support we would not be where we are now.

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