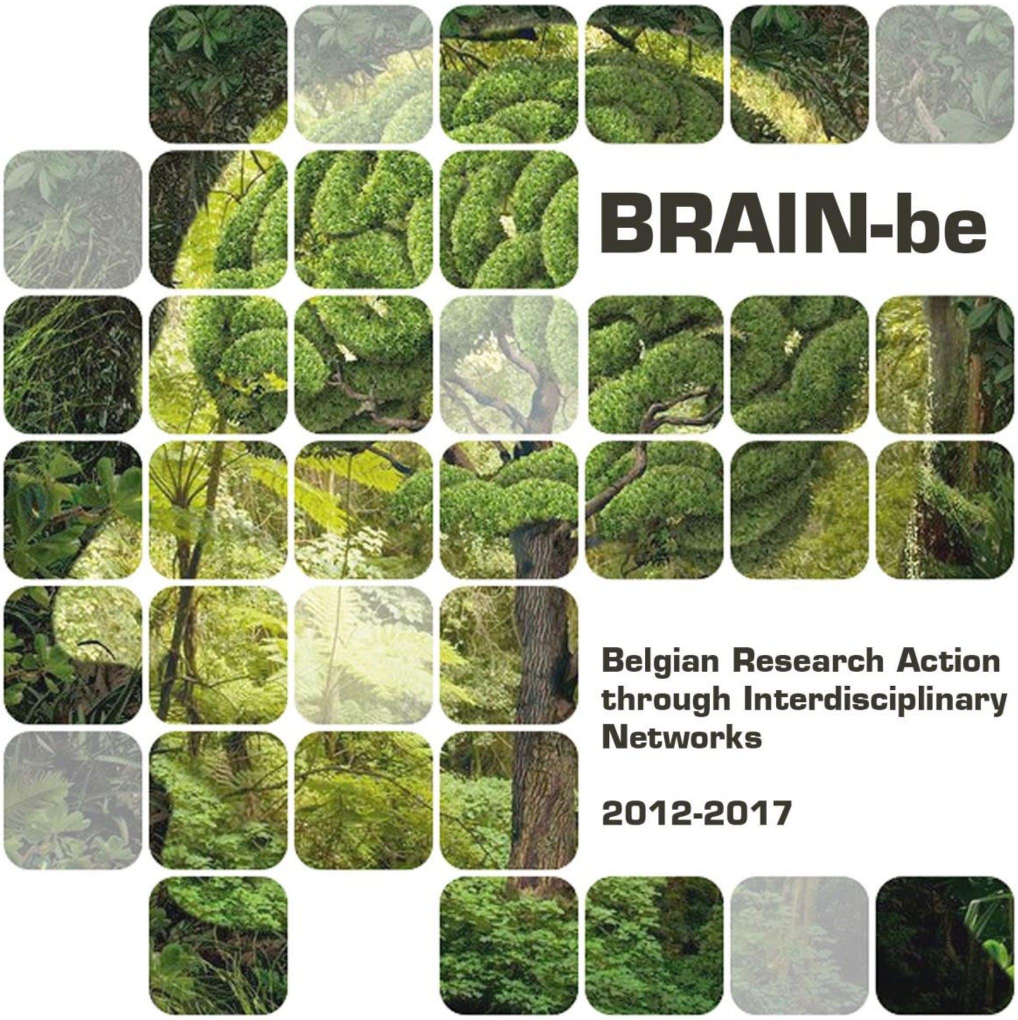

RECTO

Refugia and Ecosystem Tolerance in the Southern Ocean

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RECTO
Refugia and Ecosystem Tolerance in the Southern Ocean

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FINAL REPORT

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ABSTRACT

Context

The Southern Ocean (SO) has been isolated from the other seas of the world for millions of years, providing the stage for the evolution of endemic taxa through its long history. It is thus characterized by high levels of endemic diversity at all trophic levels. These cold-adapted marine species are threatened by global change with certain parts of Antarctica warming up at a much faster pace than other regions on Earth. RECTO used a multi-disciplinary approach, including genetic and genomic methods to construct dated phylogenies, reconstruct population histories and study phylogeographic patterns. Trophic niches were estimated with stable isotope analyses and potential adaptive evolution was tested by analyzing key morphological characters and mapping these on dated phylogenies. Dynamic energy models were developed for selected taxa while species distribution models based on existing occurrence data modelled the current and future distribution of selected taxa under different climate scenarios. A hydrodynamic ocean current model based on COHERENS was developed for part of the Southern Ocean to simulate the dispersal of marine taxa with particle modelling.

Objectives

RECTO assessed the adaptive capacities of key taxa to future climate change in the SO with six objectives: (1) Reconstructing population histories and phylogenies of selected faunas; (2) Linking population histories and refugia to past climate changes. (3) Estimating variation of morphological traits and width of ecological niches; (4) Using physiological and energy limits and traits to model current and future species distributions; (5) Integrating distribution models into hydrodynamic and particle models; (6) Developing different scenarios on how target taxa will respond to future climate change.

Conclusions

Expeditions: The RECTO consortium successfully organized a sailboat expedition to Antarctica as nimble and sustainable research platform and the first participation of Belgian scientists in a Peruvian cruise. There were also two visits of RECTO researchers to the Belgian Princess Elisabeth Station to monitor snow petrels but also successfully attempt to acquire marine samples from the ecologically important Princess Ragnhild coast while based at the station.

Methods: The research methods applied in RECTO made many important contributions to science, including for example advancing integrative taxonomy of Antarctic organisms and generating several field guides. RECTO also significantly increased molecular resources in open access databased: thousands of DNA barcodes and 20 novel mitogenomes from Antarctic amphipods, bivalves and sea stars were assembled and annotated, which will be very useful for future phylogenetic and molecular research. A protocol for the application of modern population genomic techniques to a wide variety of Antarctic organisms with reduced representation sequencing was developed and successfully applied. RECTO also developed methods to use historic samples from collections for stable isotope and microbiome analyses. Integrative phylogenetic methods were further developed and applied to understand macroevolution and adaptation of Antarctic fish and amphipods. Physiological experiments in long and short term were successfully conducted to investigate the effects of ocean acidification on sea stars and sea urchins which are expected to be hypersensitive to lower pH because of their calcite skeleton. RECTO also made huge advancements in developing Dynamic Energy Budget

and Species Distribution Models for Antarctic organisms to predict current and future physiological performance and distribution under different climate change scenarios. An oceanographic model for the SO was successfully developed from the COHERENS model to simulate larval transfer and genetic connectivity of various marine Antarctic taxa, also under different climate scenarios.

Scientific results: *1. Genetics* - We could confirm additional cryptic diversity in amphipods, echinoderms and fishes increasing standing estimates of biodiversity and indicating localized genetic variation that needs to be taken into account when designing protected areas. Genetic data also showed that the target organisms of RECTO survived past glaciations in different refugia – we found evidence for all types of refugia as suggested by Allcock & Struggnell (2012) and additional indications for multiple refugia. We also observed that even closely related Antarctic species survived in different Pleistocene refugia. These results have important implications for the possible future survival or extinction risk in view of climate change. We observed recent population expansions in certain taxa, indicating population bottlenecks in the past; if these populations would continue to expand during global warming remains to be studied. Based on DNA sequence data from population genomic approaches and mitogenomes, we found genetic differentiation between populations from the Western Antarctic Peninsula AP and Western Southern and also Eastern Antarctica in several taxa (bivalves, amphipods, fish); this implies local endemicity and local adaptations, which are not only important to include for developing suitable conservation management plans but will also increase the risk of extinction of these taxa under climate change.

We conducted the first studies on population size and genetic connectivity of snow petrels at the Belgian Princess Elisabeth Station– the population is much larger than expected and genetically formed one large population with regular genetic exchange. While trophic niches of juvenile birds were similar, those of adult birds differed, indicating different overwintering areas and different prey.

2. Microbiome - The first study of the microbiome of historic and recent samples of Antarctic fish indicated shifts of the microbiome composition through ontogeny and between different decades. Comparing microbiomes between historic and contemporary samples confirmed possible drastic intestinal microbiome changes of *Trematomus* in the last century.

3. Trophic ecology and macroecoloy - Contrary to what was known from sea stars from temperate environments, we found that sea stars in the SO had a great trophic diversity and were not always top predators. Depth and body size were the main factors influencing their trophic ecology. Such trophic diversity is important to predict the sensitivity of sea stars to future environmental changes. We also discovered that the absence of seasonal sea ice breakup caused the simplification of the food web in Eastern Antarctica illustrating that the expected sea ice changes due to climate change could have huge effects on the benthic food webs and the ecosystem functioning of the SO.

By investigating head shape disparity and constructing dated phylogenies of Antarctic *Trematomus* fish, we found support for the adaptive nature of *Trematomus* diversification and fast speciation, which could both have important implications for future adaptations of these taxa under global change. During evolution of Antarctic sea stars and amphipods, diversification mostly occurred in the last 5 million years. Such “rapid” evolution could explain the existence of many species complexes and be attributed to a diversity pump through the impact of glacial-interglacial cycles. These results illustrate that speciation and adaptation in the Southern Ocean is slow and takes millions of years.

4. Physiology - Studying the possible effects of ocean acidification on echninoderms indicated that juveniles would be expected to suffer because they remained exposed to low pH in the boording pouch during their development.

5. Modelling - Ecological modelling and physiological experiments both showed that invasive species like the Patagonian crab can reach Antarctica at the latest in 2100. Oceanic modelling furthermore illustrated that the risk for the introduction of such alien species through ballast water can be reduced if ships exchange ballast water at least 200 nautical miles from the coast.

Methods for ecological modelling were greatly improved throughout the RECTO project but it was also concluded that models at the scale of the entire SO are not meaningful due to the low quality (patchiness) of species occurrence and environmental datasets. Species Distribution Models (SDMs) should better be run at regional scales; unfortunately, current IPCC scenarios are not well suited to study species ecology because of their course spatial resolution. This makes it also difficult to link them to regional SDMs to predict responses of species to future climate change scenarios. We recommend to further improve the availability of open-access databases, also from campaigns, and to provide climate models at regional scales as soon as possible to allow to run more adequate models. Keeping these limitations in mind, SDMs can be powerful tools to illustrate future responses to climate change, also for managers and politicians. For example, two studies on the Kerguelen Plateau region concluded that species with narrow ecological niches and endemic species being restricted in their distribution to coastal areas were more sensitive to climate change. Another example of successfully applying Dynamic Energy Budget Models to two limbet species from Antarctica and regions with higher temperatures showed that almost all the energy available in reserves was allocated to somatic maintenance and growth in the Antarctic species, and little to reproduction. This explained the 40 times lower reproduction rate while also the capacity to assimilate resources was estimated to be 10 times lower in the Antarctic species, resulting in a 2.5-fold lower growth rate.

6. Validation and outreach - Besides advancing methods from multiple disciplines and producing highly interesting scientific results, RECTO was also an extremely successful project concerning validation and outreach: it produced so far 58 A1 publications, nine published data papers, and countless press releases and other activities to inform the public about the project and its expeditions and scientific results. 63 students and young researchers were supervised and trained, and 82 posters and talks presented at national and international conferences. The RECTO consortium was also closely involved in the organization of the international SCAR Biology meeting in Belgium in 2017.

7. Additional recommendations - The enormous success of RECTO illustrates the potential of a large integrative and multidisciplinary project with multiple Belgian partners as core to attract students and young researchers, to significantly advance science and provide suitable suggestions for science policy and management on conservation strategies for the Southern Ocean. Based on this experience, we recommend that funding possibilities for such large projects remain available in the future from Belspo as these provide opportunities to include teams from all three Belgian research communities.

Keywords

Keywords: Southern Ocean, refugia, trophic ecology, species distribution modelling, dynamic energy budgets, macroevolution, particle modelling, invasive species

1. INTRODUCTION

The RECTO project was funded by the Belspo BRAIN programme, ran from 2015 to 2022 and involved six Belgian partner institutions and several international partners (through sub-contracting; Museum of Natural History, Paris, France; British Antarctic Survey, UK; Alfred Wegner Institute, Bremerhaven, Germany, University of Bourgogne Franche-Comté, France). The RECTO consortium included as principal investigators Isa Schön (coordinator) and Anton Van de Putte (both at OD Nature, Royal Belgian Institute of Natural Sciences, Brussels (RBINS)), Bruno Danis, Chantal De Ridder, Philippe Dubois (Marine Biology Lab, Free University of Brussels (ULB)); Gilles Lepoint and Bruno Frederich (MARE Centre, Laboratory of Oceanology, University of Liege (ULg)), Marc Kochzius (Marine Biology, Free University of Brussels (VUB)); Ann Vanreusel and Frederik Leliaert (Marine Biology Research Group, Ghent University) and Filip Volckaert (Laboratory of Biodiversity and Evolution, KU Leuven (KUL)).

As its title indicates, RECTO set out to study refugia and ecosystem tolerance in the Southern Ocean (SO), investigating six different animal groups comprising different trophic levels from benthos to top predators and including crustaceans (ostracods, amphipods), echinoderms (sea stars and sea urchins), bivalves, fish and snow petrels. RECTO applied a multidisciplinary approach combining genomic data with morphological, phylogenetic, coalescent, fossil, ecological and oceanic modelling approaches.

2. STATE OF THE ART AND OBJECTIVES

The SO had a long history of millions of years (Clarke & Crame 2010, Lawver et al. 2014) which has facilitated the evolution of many endemic species (De Broyer et al. 2011, 2014, De Broyer & Danis 2013). Major climate changes in the past (Zachos et al. 2008, Convey et al. 2014) including the most recent Pleistocene glaciations disrupted life on the continental Antarctic shelf (Huybrechts 2002) and triggered different responses in marine organisms. While some species survived in situ (Barnes & Kulinski 2010), others found refugia elsewhere (Allock & Strugnell 2012). Genetic studies suggest that the deep-sea (Dambach et al. 2012), parts of the Antarctic shelf (Hemery et al. 2012) and the seas of sub- (Fraser et al. 2012, Hemery et al. 2012) or peri-Antarctic regions (e.g. Gonzalez-Wevar et al. 2013,) provided refugia from where populations expanded post-glacially.

The ecosystems of the Southern Ocean (SO) are currently exposed to a combination of environmental stressors through global change including increasing temperature, UV exposure and acidification of seawater, causing collapsing of ice shelfs, retreating of glaciers and subsequently changes of the sea-ice conditions (Fabry et al. 2009, Reygondeau et al 2014, Gutt et al. 2015, Menezes et al. 2017, Etourneau et al. 2019). Currently, the Western Antarctic Peninsula (WAP) is exposed to the most intense environmental changes (Kerr et al. 2018, Siegert et al. 2019) with a strong expected impacted on marine ecosystems (Figure 1). The unique characteristics of Antarctic organisms, such as high levels of endemism (Griffiths et al. 2009, Kaiser et al. 2013, Saucede et al. 2014), and being very sensitive to increasing temperatures (Cheng & William 2007, Pörtner et al. 2007, Peck 2016, Peck et al. 2018) are expected to further increase the potential vulnerability of organisms, their populations and also the ecosystems of the SO (Peck 2004, Peck et al. 2004, 2010, Ingels et al. 2012, Lohrer et al. 2013, Guillaumot et al. 2018b). Our knowledge of Antarctic ecosystem responses to these global change remains patchy calling for additional investigations (Sen Gupta et al. 2009, Sewell and Hofmann 2011; Constable et al. 2014, Reygondeau et al. 2014, Bonsell & Dunton 2018, Le Guen et al. 2018, Rogers et al. 2020).

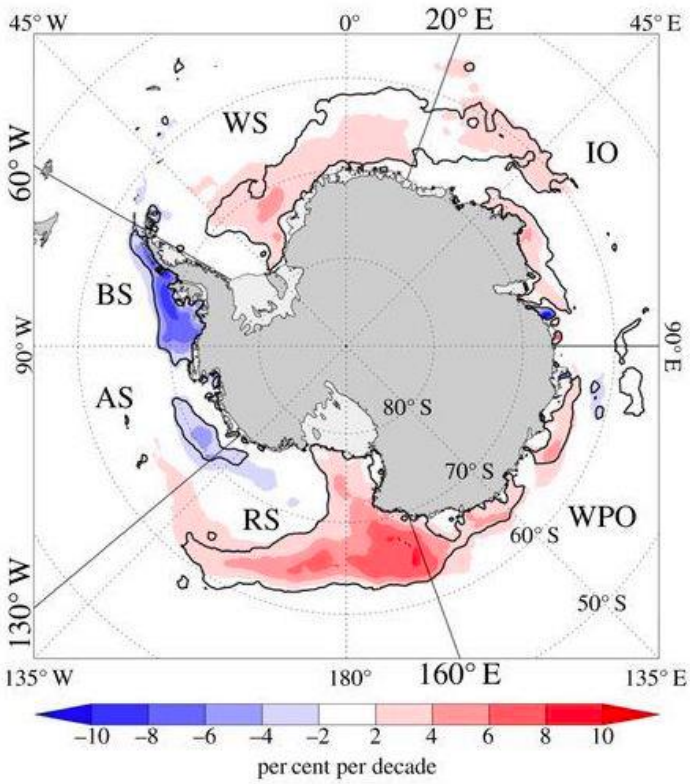


Figure 1: Map of Antarctica indicating the trends in the mean SIC for 1979–2013 (per cent per decade). Areas with a significant trend are enclosed by a bold line (Turner et al. 2014).

Besides reconstructing refugia and evolutionary histories, molecular data can also be used for barcoding and the identification of cryptic genetic diversities. DNA barcoding is a well-established method to verify taxonomic identifications of animals through the use of short DNA sequences; most commonly the cytochrome oxidase I (COI) subunit gene (Hebert et al. 2003). The method has been applied for the identification of Antarctic fauna before (e.g. Schiaparelli et al. 2013, Lautredou et al. 2010, Krabbe et al. 2010, Havermans et al. 2011, Allcock et al. 2011) and is relatively straightforward to use, provided that sufficient reference database material is available (Ratnasingham & Hebert 2007). The same method can also be applied to identify cryptic thus hidden genetic diversity, which is known to occur in various marine taxa (Bucklin et al. 2011, Fontaneto et al. 2015), also in the SO (see for example Brandão et al. 2010, Brasier et al. 2016, Dornburg et al. 2016, d'Udekem d'Acoz et al. 2018, Zbawicka et al. 2019). Including data on such cryptic diversity provides more realistic estimates for biodiversity and helps to assess ecosystem functioning.

We can. Now generate high-resolution molecular data to study past and current adaptations and reconstruct population histories. These novel methods applying genome reduction through the fragmentation of the genome with restriction enzymes were developed with a first focus on model animals of genetic research (Baird et al. 2008) and plants (Elshire et al. 2011). Subsequently, these methods have been improved and refined and many varieties of similar protocols mostly aiming at reducing costs and increasing flexibility were published (e.g. Hoffberg et al. 2016). These methodological varieties all follow the same principle and can be summarized under the umbrella term reduced representation sequencing (RRS; Campbell et al. 2018). Countless studies demonstrated new insights for both non-model and model organisms using RRS methods (e. g. Andrews et al. 2016, Fang et al. 2018, Xuereb et al. 2018). However, inappropriate methodological choices especially when studying non-model organisms with limited genomic resources can lead to inefficient resource use, or worse, false biological inferences (Lowry et al. 2016). Antarctic research so far benefited very little from the potential of well-designed RRS experiments (but see e.g. Galaska et al. 2017, Humble et al. 2018) and caveats were identified, for example in Antarctic krill, because of the large amount of repetitive regions in the genome (Deagle et al. 2015), which still need to be overcome.

Antarctic taxa have obviously adapted to past environmental changes through various strategies. The ability to seek refugia is strongly influenced by habitat and dispersal capacity, which may vary throughout life (Fraser et al. 2012), and by plasticity and ecological adaptability. For example, all *Pygoscelis* penguins expanded their populations after past glaciations but only Southern Gentoo penguins show similar range expansions today (Clucas et al. 2014). These different fates were attributed to ecological differences, with the winning Gentoo penguins having more diverse and flexible foraging niches. Such knowledge on past and present adaptations is crucial to predict responses to future climate changes (Fraser et al. 2012). Global change is quickly affecting planet Earth, and parts of Antarctica are among the fastest warming regions (Turner et al. 2014, Bromwich et al. 2013) while the SO is also endangered by ocean acidification (OA). Antarctic adult echinoderms were hypothesized to be particularly vulnerable to OA due to their low metabolism - associated to a supposed poor machinery to eliminate CO_2 and protons - and heavily calcified high-magnesium calcite skeleton (McClintock et al. 2011, Sewell & Hofmann 2011). However, the few available studies on Antarctic echinoderms reported contrasted responses and indicated that they might be more tolerant than expected, at least at the adult stage (Ingels et al. 2012, Constable et al. 2014, Morley et al. 2016, Peck et al. 2018). No data were available on the acid-base response to OA or on the effects of this on the skeleton of Antarctic and Subantarctic echinoderms, which is considered at risk by many authors (McClintock et al. 2011, Sewell & Hofmann, 2011, Duquette et al. 2018). As in other parts of the world, the SO is challenged by intense environmental changes. These changes occur with important regional variations (Meredith & King 2005, Martinson et al. 2008, Convey et al. 2009). In the near future, meta-analyses of several global climate models are predicting continuing atmospheric and oceanic warmings of several degrees (Walsh 2009, Bracegirdle & Stephenson 2012, Mayewski et al. 2015). These climate models (CMIP5, Coupled Model Intercomparison Project) defined four RCP scenarios (Representative Concentration Pathways, 5th report 2013) that placed the assumptions on different greenhouse gases emissions in the atmosphere in coming decades between moderate (RCP 4.5) to business-as-usual (RCP 8.5) scenarios (Turner et al. 2014, Liu & Curry 2010).

Impacts on organisms of these cascading environmental changes were already recognized (see Convey & Peck 2019 for a review) and included studies on fish (Bilyk & DeVries 2011, Strobel et al. 2012), molluscs (Clark et al. 2008, Peck et al. 2007, Reed & Thatje 2015), echinoderms (Peck et al. 2009a, Morley et al. 2016), isopods (Young et al. 2006, Janecki et al. 2010), Foraminifera, Nematoda, Amphipoda (Ingels et al. 2012) and sponges (Fillinger et al. 2013). Warming temperatures directly reduced species survival (Peck et al. 2009b, Morley et al. 2009a, 2010, Peck 2011, Navarro et al. 2020), as biological functions such as feeding, rasping, swimming activities or even respiration were strongly constrained by temperature elevation (Peck et al. 2004, Morley et al. 2009b). Moreover, ocean warming reduced oxygen availability for marine organisms, as oxygen concentration is lower in warmer waters (Benson & Krause 1984, Peck & Uglow 1990). These changes affected species to correctly produce energy to maintain (in this context of increased metabolic rates) without using anaerobic processes that induce toxic end products (Peck 2005, Pörtner et al. 2007). In addition, the combined effect of altered sea ice dynamics and increased meltwater runoffs, with wind patterns and oceanographic conditions had an unprecedented impact on plankton communities, with declining habitat suitability (Whitehouse et al. 2008), inducing shifts in dominating species within planktonic communities which are likely to modify relative species abundances (Whitehouse et al. 2008, Montes-Hugo et al. 2009, Schloss et al. 2012, Schofield et al. 2017), and consequently, also altering community assemblages (Moline et al. 2004, Ashton et al. 2017), functions (Braeckman et al. 2021) and predator-prey interactions in food-webs (Michel et al. 2019).

Future distributions of SO taxa under different scenarios can be predicted by integrating spatial and trait distribution models based on physiological limits and ecological niches with state-of-the art models for ocean dynamics (Luyten 2011), sea ice (Vancoppenolle et al. 2009) and Lagrangian particle models (Dulière et al. 2013).

Objectives

RECTO assessed the adaptive capacities of key taxa to future climate change in the SO with the following six objectives:

1. Reconstruct population histories and phylogenies of selected faunas

2. Link population histories and refugia to past climate changes

3. Estimate variation of morphological traits and width of ecological niches

4. Use physiological and energy limits and traits to model current and future species distributions

5. Integrate distribution models into hydrodynamic and particle models

6. Develop different scenarios on how target taxa will respond to future climate change

3. METHODOLOGY

3.1 Expeditions and sample acquiring

Members of the RECTO consortium participated in three kinds of expeditions: (1) expeditions to Antarctic stations where population biology and physiological research was conducted and bird and marine organisms were sampled; (2) on large scientific vessels where epibenthic sledges, amphipod traps and grabs were deployed to sample a wide range of marine organisms; and (3) the Belgica121 expedition (B121) venturing to explore the marine biodiversity of the West Antarctic Peninsula from 23.2.2019-24.03.2019 to test the concept of using a nimble sampling platform, the R/V Australis, a steel hulled, fully rigged motor sailor.

More details of the expedition results can be found below (4.1).

3.2 Patterns of evolutionary diversifications and morphological analysis

During the RECTO project, we developed multiple strategies to collect morphological data for studying patterns of evolutionary diversifications in selected animal groups. We used (1) published data as they are often available in taxonomic reviews and species descriptions; (2) museum specimens; and (3) specimens collected in past Antarctic expeditions. This approach allowed us to have access to a very large collection of specimens from many species but also to obtain information about intra-specific variation. We focused studying morphological diversity on Antarctic fish and amphipods. Photographs and stack images from lateral view as well as micro-CT scans of specimens were used to collect ecologically relevant measurements in amphipods and cryonotothenioid fishes (e.g. eye size, body length, body height, body width…). Shape analyses were also performed using landmark-based geometric morphometric methods (Zeldtich et al. 2012).

For the amphipods, discrete traits (presence/absence of trait such as type of eye, body tooth pattern…) were collected by an extensive literature review. Stack images were obtained for 131 specimens from 13 *Eusirus* species. Representatives of Epimeria (146 specimens from 38 species) and Iphimediidae (244 specimens from 37 species) were also scanned to provide 3D shapes and scans of morphological attributes.

For the cryonotothenioid fishes, morphological data were collected from specimens originating from museum collections and field expeditions. The images of 193 specimens from various Notothenoids, mainly Trematominae (11 species), were collected in the museum collections of Paris (MNHN) and London (NHM). Two Master students (Quentin Peignot & Nicolas Gamb) photographed and measured various morphological traits on specimens from the Antarctic Circumnavigation Expedition (ACE), the expedition Antarktis XIX/5 & XXI/2, and the expedition PS96 ANT-XXXI (Frédérich et al. 2022).

3.3 Molecular methods

3.3.1 Integrative taxonomy, DNA barcoding and mitochondrial genomes

Classic taxonomic research and integrative taxonomy (combining classic approaches with molecular data) were applied to several of the RECTO target organisms, including amphipods, fish and sea stars. For the six different animal groups which RECTO has studied, thousands of DNA extractions and DNA barcodes were also generated. DNA barcoding was used to verify taxonomic status of fish specimens and scan for potential unrecognized or cryptic species, including verifying visual fish specimen identifications (Christiansen et al. 2018, Heindler et al. unpublished, Christiansen et al. unpublished). Molecular verification uncovered misidentifications in virtually all tested Antarctic fish sample collections, even if at a low rate. In many cases these misidentifications were easy to correct and thus made these specimens amenable for further research. Generally, some species and specimens were more prone to misidentification such as early life stages, morphologically similar species, or species that lose taxonomically informative characters upon capture (Christiansen et al. 2018). DNA barcoding was also used to extend publicly available databases and screen for phylogeographic patterns and cryptic species specifically in mesopelagic fishes of the Southern Ocean (Christiansen et al. 2018).

As a newly developed part of the RECTO project, the KU Leuven team further extended barcoding techniques to study the diet and microbiome of Trematomid fish from recent and historic samples (Heindler et al. 2018). Below, the results of this approach are described in more detail (4.4.1).

By conducting low coverage whole genome sequencing at the Genomics Core of the KU Leuven and in collaboration with the Agnes Dettai from the MNHM in Paris using Illumina sequencing technologies of long-range mitochondrial PCR products, the RECTO consortium successfully generated complete mitochondrial genome data from a wide range of target organisms, including Antarctic amphipods, sea stars, bivalves, and fish (see below). All of these mitogenomes are new – for Antarctic amphipods for example, up to now only a single complete mitogenomes was published (Shin et al. 2012). RECTO generated three additional complete mitogenomes from Antarctic amphipods with full assembly and annotation. Likewise, for the bivalve *Aequiyoldia eightsii* the mitogenome could be assembled as well as for 16 sea stars species; the latter data were shown to be essential for solving long-standing taxonomic and evolutionary debates. For the bivalve *Laternula elliptica*, large parts of the mitogenome sequence data could be successfully sequenced; these data were used for phylogeographic studies and reconstructing post-glacial refugia (see results below). The low coverage sequencing approach was only unsuccessful for ostracods where suitable reference genomes of sufficiently close relatives were lacking to map sequencing reads, while for snow petrels, the number of reads was too low to successfully assemble the mitogenome, probably because of the whole genome size of this bird species of around 2Gb (Christiansen et al. 2021).

3.3.2 Reconstruction of population histories and population connectivity with molecular methods

RECTO pioneered the use of reduced representation sequencing (RRS) methods for Antarctic animal taxa (Christiansen et al. 2021). We designed a large pilot experiment to test and streamline the applicability of RRS to Antarctic animal taxa (Christiansen et al. 2021), also in the most time- and cost-efficient way. Under the lead of the KUL partner and involving all other project partners, the RECTO consortium tested different RAD protocols using a mix of bioinformatic simulations and molecular approaches and successfully fine-tuned and optimized RAD-sequencing methods for four of the six RECTO target animal groups, namely fish, sea stars, bivalves, and ostracods (Christiansen et al. 2021). Because of too variable and possibly huge genome sizes, amphipods were not included in the test sequencing runs for the final optimization; for them, other molecular approaches were proposed (Christiansen et al. 2021) until exact estimates of genome sizes will become available for. Applying the optimized protocol produced inadequate sequencing results for the snow petrel samples, probably because of degenerated DNA due to non-invasive sampling. Microsatellites (see below) or other protocols for DNA extractions will need to be further developed for these birds in the future. It is the first time that such an optimization was successfully achieved for such a wide taxonomic range of animals; the manuscript was published in the open access journal BMC Genomics in 2021 and its approach was already successfully applied to the sea star *Bathybiaster loripes* (Astropectinidae) for which more than 15,000 polymorphic loci for 114 specimens were generated (Jossart et al. in prep.) to test the depth differentiation hypothesis (Moreau et al. 2019) and to the bivalve *A. eightsii* (Van Craenenbroeck et al. in prep.).

3.4 Stable isotope measurements and modelling

Measurements of stable isotopes ratios of carbon (C), nitrogen (N) and sulfur (S) were performed using EA-IRMS on thousands of tissue samples from invertebrates (including 2500 seastars (PhD thesis of Baptiste Le Bourg) and amphipods) and vertebrates (fish and birds). Generated data encompassed all trophic level from primary producers to third level consumers. These data were explored using Bayesian isotopic niches modelling and mixing model. Two trophic webs were extensively studied during a campaign in Dumont d'Urville station (East Antarctica) and Kerguelen Island with a focus on habitat dominated by kelp (Michel et al. 2019; Le Bourg et al. in preparation). Additional tests on tissues with different fixation methods confirmed the usefulness of samples preserved in alcohol or formaldehyde for stable isotopes analysis, opening the possibility to use historic collections for this kind of analysis in future research (Le Bourg et al. 2020). Applying novel protocols from this approach, stable isotope analysis was used to explore trophic diversity and plasticity of seastars, allowing to gather samples from all around Antarctica collected between 1985 and 2017. Amphipods were also targeted focusing on the genus *Eusirus* (PhD thesis of Louraine Salabao,) and the Iphimediidae family (Marie Verheye, FNRS Post-doc). For such small animals, using only a single appendix (i.e. pleopod) was sufficient to measure stable isotope ratios of C and N and preserve the remaining specimens for taxonomic studies. For amphipods, isotopic information was combined with genetic and morphological data to assess the eco-evolutionary history of these taxa. Also for fish, we combined isotopic, genetic and morphological data to explore the variability of these characters in an eco-evolutionary context. We realized hundreds of stable isotope measurements of ice fishes caught during diverse campaigns. Genetic and morphological data were also generated from museum specimens (Heindler et al. 2018, Frédérich et al. 2022). Finally, stable isotopes (C, N and S) measurements on the snow petrel *Pagodroma nivea* sampled close to the Princess Elisabeth Belgian polar station during a BELAERE expedition (H Robert, 2017-2018) were performed on feathers, bones and muscles to compare individual trophic ecology (n = 150 individuals) in different temporal frames. Mercury was measured as well to assess possible contamination.

Stable isotope data for seastars are available at
https://doi.org/10.1594/PANGAEA.906520 (Le Bourg et al. 2019) and
https://ipt.biodiversity.aq/resource?r=antarctic_subantarctic_asteroidea_isotopes&v=1.2 (Moureau et al. 2021) for experimental and field work. Data generated by the Dumont d'Urville campaign are available at: https://ipt.biodiversity.aq/resource?r=ddu_isotopes_verso_2013_2015&v=1.1 (Michel 2019). Other data sets are planned to be published in open access as soon as possible.

3.5 Macroevolutionary research

We studied the evolutionary history of two taxonomic groups for which phylogenetic hypotheses were already available: cryonotothenioid fishes as well as *Eusirus*, *Epimeria* and Iphimediidae amphipods. These tasks required an integrated phylogenetic approach with cutting-edge methods, including for example micro-CT scans of amphipod appendages, in combination with ecological, isotopic and phylogenetic data (see below).

3.6 Physiology

Field experiment

Here, for the first time, the opportunities offered by the shallow hydrothermal vent activities in Deception Island Caldera (Antarctic Peninsula) were used to assess the life-long impact of ocean acidification on the sea urchin *Sterechinus neumayeri* and the sea star *Odontaster validus* (in collaboration with the University of Barcelona, Prof. Conxita Avila and Dr Carlos Angulo-Preckler). The two species were sampled in four stations within the Caldera, two at pH (total scale; pH_T) 8.0- 8.1 and two at reduced pH 7.8. Measured variables included pH_T, alkalinity, and dissolved inorganic carbon of the coelomic fluid; characteristic fracture force, stress and Young's modulus using Weibull statistics and Cd, Cu, Fe, Pb and Zn concentrations in the integument, gonads and digestive system.

Aquarium experiment on O. validus

Odontaster validus individuals were collected at McMurdo station in November 2016. 600 individuals were brought to the special containment lab at Portobello station (University of Otago) and set-up in refrigerated cabinets. The experiment consisted of a long-term exposure (2 years) of these individuals to a combination of food levels (starvation, sporadic feeding), temperature (0, 1, 2, 3 and 4°C) and pH_T (ambient 8.15 and reduced 7.6) (in collaboration with Otago University, New Zealand, Prof. Miles Lamare). Every 6 months, metabolic rate was measured in 4 individuals of each treatment combination. These individuals were dissected afterwards. Proximal data including gonad index, pyloric index, body wall index, ash content were obtained. Sections of the gonad were preserved for histological analyses. Sections of the body wall were preserved for biomechanics studies; at 0, 6 and 12 months pH_T, alkalinity, and dissolved inorganic carbon of the coelomic fluid were measured. At 24 months, eggs were obtained by immersion of female gonads in 1µM 1-methyladenine. Sperm was obtained from dissected testes and diluted in filtered seawater to fertilize the eggs. Cultures were started with larvae originating from individuals kept at temperatures 0, 1, 2 and 4, and ambient pH_T. Samples of eggs from the different treatment combinations were collected for biochemical analyses (protein, lipid classes and carbohydrates composition).

Aquarium experiment on A.cordatus in Kerguelen Islands

Sea urchins were progressively exposed to pH_T 8.3 (current value in Kerguelen Islands), 8.0, 7.7 and 7.4 (in collaboration with the University of Bourgogne Franche-Comté, Dr. Thomas Saucède). At regular intervals, sea urchins were sampled and their coelomic fluid collected in which pH_T, alkalinity, and dissolved inorganic carbon were measured.

3.7 Ecological modelling

In the framework of the RECTO project, significant efforts were also made to advance the field of SO ecological modelling, with special attention for developing integrative, predictive models at various spatio-temporal scales and also improving the methodological aspects. The most significant advances of this facet of RECTO were carried out in the framework of a PhD thesis by Charlène Guillaumot.

Due to its accessibility, our understanding of SO’s ecosystem structure and processes is fragmentary, and there is an urgent need to fill knowledge gaps. Among the avenues available to overcome this issue, modelling has been widely applied during the last two decades. Models are "purposeful representations of a system, hypothesis or experiment and include any useful form of abstraction to assist thinking" (Starfield et al. 1990). Ecological models are simple representations of a complex reality. They allow to identify drivers of species ecological niche and to improve our understanding of species responses to environmental changes. However, applying models to SO benthic organisms raises several methodological challenges. For example, data on species occurrence is often aggregated in time and space nearby research stations or along main sailing routes (Griffiths et al. 2017). Datamass is also limited leading to difficulties in accurately describing the width of both fundamental and realized ecological niches. In this part of the project, we focused on modeling both types of niches.

To model the fundamental niche, we used DEB theory, that defines individuals as dynamic systems and provides a mathematical framework for the life cycle of an organism. The theory describes the physiological processes with four primary state variables: reserve, structure, maturity and reproduction buffer (the latter for adults only), directly linked to mass and energy flows and influenced by two forcing environmental variables: temperature and food resources availability (Fig. 0.9, Kooijman 2010). DEB theory relies on key concepts such as consistency with biological and ecological principles, as well as first laws of thermodynamics for conservation of mass, energy and time (Jusup et al. 2017) and assumes that the various energetic processes, such as assimilation and maintenance rates are dependent either on surface area or on body volume (van der Meer 2006).

To model the realised niche, we applied Species Distribution Modelling (SDM) also (inadequately) known as ecological niche modelling, habitat suitability modelling or climate envelope modelling (Austin 2002, Pearson 2007, reviewed in Sillero 2011). SDM is based on a statistical relationship between occurrence records and environmental data (Elith et al. 2006, Elith and Leathwick 2009, Peterson et al. 2011). Environmental conditions at the location of available presence-only (or presence-absence) data are extracted to generate a matrix used to build the SDM. The complexity of the relationship between occurrence records and environmental conditions is conditioned by the chosen mathematical representation of the SDM (i.e. the model algorithm: linear or polynomial relationships, classification trees, entropy minimisation) (Elith and Leathwick 2009, Anderson 2013). Model outputs that represent the probability distribution of the species are projected on a geographic and/or climatic/environmental space to identify areas where the environment fulfills the required environmental conditions (Anderson 2013).

3.8 Oceanic modelling

For the planned oceanic modelling, the model grid and bathymetry were finalized and implemented in the COHERENS hydrodynamic model for the SO. 19 tidal harmonic constituents were extracted from the FES2014a ocean tide model results, interpolated over the model grid and implemented in the model to provide tidal harmonic information at the ocean open boundaries. A new scheme for isopycnal diffusion was included in COHERENS and model boundary conditions were adapted to a curvilinear grid.

The tracer module of COHERENS was set up in a standalone mode, using hydrodynamic parameters produced by the Operational Mercator global ocean analysis and forecast system (Law Shune et al. 2019) and made available via the Copernicus data portal (http://marine.copernicus.eu/). These data comprise daily average values of sea surface elevation and horizontal ocean currents plus information on sea ice, the potential temperature of sea water, sea water salinity and mixed ocean layer thickness.

Daily averaged model parameters were generated after interpolation from the native model grid to a global standard Arakawa C grid with 1/12° horizontal resolution and 50 fixed vertical levels ranging between 0 and 5,000 m. 3D vertical ocean currents were estimated from divergence in the horizontal velocity from the 2008-2016 Operational Mercator PHY_001_024 forcing fields, assuming null surface and bottom vertical velocity.

This approach provided the following advantages for a successful application of the model for RECTO: (1) it ensured the availability of hydrodynamic forcing essential to perform dispersal simulations, (2) it reduced the computation time and, (3) it gave the opportunity to enlarge the model spatial domain (Figure 2). Main disadvantages were the dependency on global ocean datasets and the lower flexibility to perform simulations with future or past climate scenarios. The model was validated and successfully applied to different scenarios. These included so far modelling the ability of potentially invasive organisms in ship ballast water to reach coastal areas of the Western Antarctic Peninsula (Guillaumot/Duliere et al. 2022), comparisons of larval dispersal and population genetic patterns in Antarctic fish *Trematomus eulepidotus* and *T. loennbergii* (Christiansen et al. in prep.) and the bivalve *Aequiyoldia eightsii* (Van Cranenbroek et al. in prep.), and the potential dispersal of the invasive Patagonia crab species *Halicarcinus planatus* (Guillaumot/López-Farrán et al. submitted).

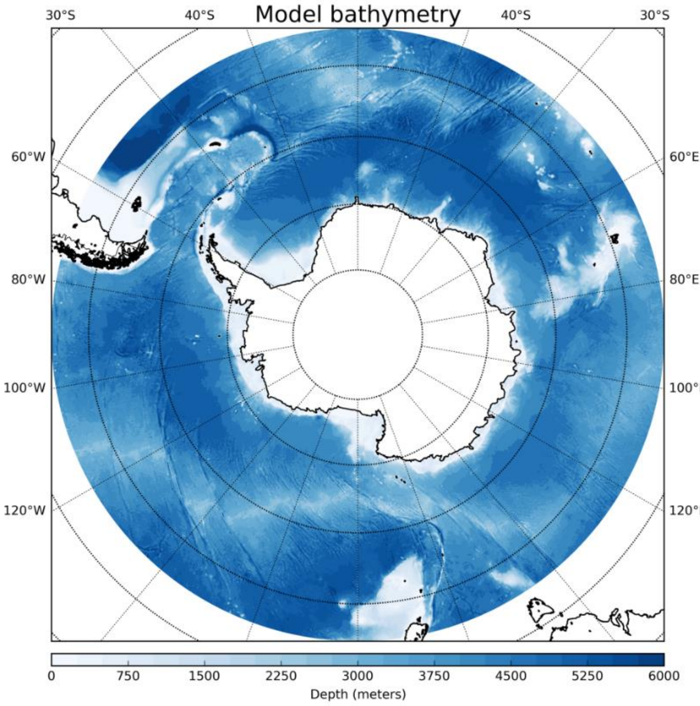


Figure 2: Dispersal model domain and bathymetry of the oceanic model for the SO.

4. SCIENTIFIC RESULTS AND RECOMMENDATIONS

4.1 Expeditions and sample acquiring

4.1.1 Expeditions to Antarctic stations:

- BELAERE 2021-2022: Bruno Danis (ULB) successfully participated in the BELAERE 2022 mission to Princess Elisabeth Station in early 2022. For the first time, the Princess Ragnhild Coast in East Antarctica (region of Breid Bay and Camp Derwael) was sampled, which is located nearly 200 km from the station, and has been identified to have a high ecological value for birds and mammals (top predators in the marine food chain; see http://www.antarcticstation.org/news_press/news_detail/recto_project_sets_stage_for_future_biological_research for more details). The aim was to identify the characteristics of the terrain and the challenges to conduct marine biodiversity research from the station. Baited traps and a lander with light harvesting gear were successfully deployed although some difficulties arose with the underwater lighting and picture shooting system. Nevertheless, a series of oceanographic measurements could be done with a CDS to characterize the region for future marine research. Bruno Danis also explored the access to the snow petrel populations in the vicinity of the station and took additional samples to test their suitability for future micobiome and genetic research

- BELAERE 2017-2018: Henri Robert went to the Belgian Princess Elisabeth station (PES), acquired more than 100 snow petrel samples in a non-invasive way and conducted the first survey of this species in the vicinity of the station in the Sør Rondane Mountains.

- Antarctic campaign Deception Island (Antarctic Peninsula) 2018: participation by Sarah Di Giglio and Philippe Pernet to conduct physiological experiments on echinoderms. (22/2/2018 - 11/3/2018).

- Antarctic campaign Scott Base (Ross Island): participation by Antonio Agüera (30/10/2016 – 10/11/2016).

4.1.2 Expeditions to the Southern Ocean with vessels:

- The expedition PS118/ANT XXXIV-3 to the SO, organized by the Alfred Wegener Institute for Polar and Marine Research (AWI), Germany, on board of their icebreaker RV Polarstern, took place between 7 February and 12 April 2019. The general aim of this multidisciplinary expedition was to collect base-line information on environmental and biological processes taking place in the area formerly covered by A-68, the 5800 km^2 iceberg which calved from the Larsen C iceshelf in July 2017. For the RECTO project, Filip Volckaert (KU Leuven) and Marie Verheye (University of Liège & RBINS) participated. They aimed to study the evolution of the benthic fauna in the Weddell Sea, focusing on amphipods (M. Verheye) and fishes (F. Volckaert), but also to provide research material for all the other partners of the RECTO project (sea stars, molluscs, ostracods, crinoids, …).

- The ANTARXXVII expedition to the Western Peninsula (Brainsfield Strait, Elephant Island, Admiralty Bay, Collins Bay, Hope Bay), was organised by the Peruvian ministry of foreign affairs on board of the icebreaker BAP Carrasco. The cruise took place from 24.12.19 to 03.03.2020 in two legs and four Belgian students, PhD student Louraine Salabao (University of Liège, University of Hasselt & RBINS), and Master students Jolien Claes, Louise Delhaye and Quentin Engelbrecht (VUB) participated. They aimed to study the benthic fauna focusing on brittle stars (J. Claes) and amphipods (L. Salabao), the community structure of benthic organisms in the Antarctic Peninsula (Q. Engelbrecht) and heavy metal accumulation in the Brainsfield Strait (L. Delhaye). They also acquired samples for the RECTO project including bivalves, sea stars, amphipods and fish. This was the first successful, joint cruise of Belgian and Peruvian (and other) scientists following the recent Memorandum of Understanding (MoU) between Belgium and Peru.

- B120/B121: The Belgica121 expedition (B121) ventured to explore the marine biodiversity of the West Antarctic Peninsula to test the concept of using a nimble sampling platform, the R/V Australis, a steel hulled, fully rigged motor sailor. Named as a tribute to the first international scientific expedition in Antarctica lead by Adrien de Gerlache in 1897-99 (onboard the Belgica), B121 took place between February and March 2019, sampling 15 stations in 22 working days in an area extending from the Berthelot (65°19.751 S, 64°08.263 W) to the Melchior Islands (64°19.246 S, 62°55.375W). Deploying 20 different types of gear (both traditional and modern), the B121 team gathered over 1700 samples that were brought back to Belgium for further identification (by taxonomic experts) and analyses (isotopes, population genetics or genomics…). The team focused on biodiversity assessments, from the intertidal to subtidal zone (20 m) in coastal areas with contrasting characteristics regarding their exposure to glaciers, oceanographic characteristics, and intensity of touristic activities. Other projects included population genetics studies, trophic ecology, environmental DNA, microplastics surveys and more (see full report & https://belgica120.be for more details). The B121 expedition on the sailboat Australis organised by Bruno Danis from ULB illustrated that such smaller cruises can be highly successful in several aspects: being much more sustainable, specifically targeting shallow coastal areas which are not usually sampled by large research vessels, employing a wide range of gears, and being flexible as the research program is planned by the participants. We would recommend that this kind of cruises is strongly supported in future Antarctic research.

- Subantarctic campaigns to the Kerguelen Islands: participation of Philippe Dubois (3/11/2016 – 31/12/2016 and 2/11/2018 - 30/12/2018)

We can conclude from our experience that the participation of RECTO scientists and students in expeditions using large research vessels strongly depended on the access granted by foreign partner institutions and organisations as for example the German AWI organising Polarstern cruise PS118, making it unpredictable for Belgian Antarctic researchers to plan future expeditions. The new MoU between Belgium and Peru will hopefully provide more structural access to the Peruvian research vessel in the future. The first experience of participating in ANTARXXVII was positive. Also the use of the sailboat Australis for Antarctic expeditions was an enormous success in terms of the number and volume of acquired samples as well as the uniqueness of the sampled areas and the attention of the public. The same approach will now be used in the BRAIN TANGO project. Also the two participations of RECTO scientists in BELAERE expeditions at the PES were successful; the second one in 2022 was the first trial to also acquire marine samples at the nearest coastline, which was mainly successful and opens opportunities for further marine research from the station.

4.2 Integrative taxonomy, DNA barcoding and mitochondrial genomes

In combination with classic taxonomic approaches, DNA barcoding data and the discovery of cryptic diversity and species complexes has led to important taxonomic revisions for amphipods (D’Udekem d’Acoz & Verheye 2017, D’Udekem d’Acoz et al. 2018), echinoderms (Moreau et al. 2018; Jossart et al. 2020) and fish (Christiansen et al. 2018). This approach has also generated much more accurate estimates of biodiversity by taking cryptic diversities into account (see examples for cryptic sea star species with common and different geographic distributions in Figure 3a-b and for cryptic species in the amphipod *Charcotia* amundseni in Figure 3c). Also most of the described species of Antarctic iphimediid amphipods appear to be complexes of multiple morphologically similar species (Verheye et al. in prep.). The integrated taxonomy results have furthermore been translated into several field guides (Feral et al. 2019, Saucède et al. 2020, Jossart et al. 2020 - pterasteridae-so.identificationkey.org) facilitating the identification of Antarctic organisms in future research. Jossart et al. (2020) combined genetics and morphology to assess the diversity of Pterasteridae, a sea star family diversified in deep-sea and polar environments. Because of their derived anatomy and the frequent loss of characters during preservation, Pterasteridae are a suitable test case for such an integrative study. The molecular identification (COI) of 191 specimens (mostly from the SO) suggested the existence of 26–33 genetic species in three genera (*Diplopteraster*, *Hymenaster* and *Pteraster*), which matched the morphological identification in 54–62% of all cases (Figure 4). The mismatches were either different molecular units that were morphologically indistinguishable (e.g. *Pteraster stellifer* units 2 and 4) or, conversely, nominal species that were genetically identical (e.g. *Hymenaster coccinatus/densus/praecoquis*) (Fig. 4).

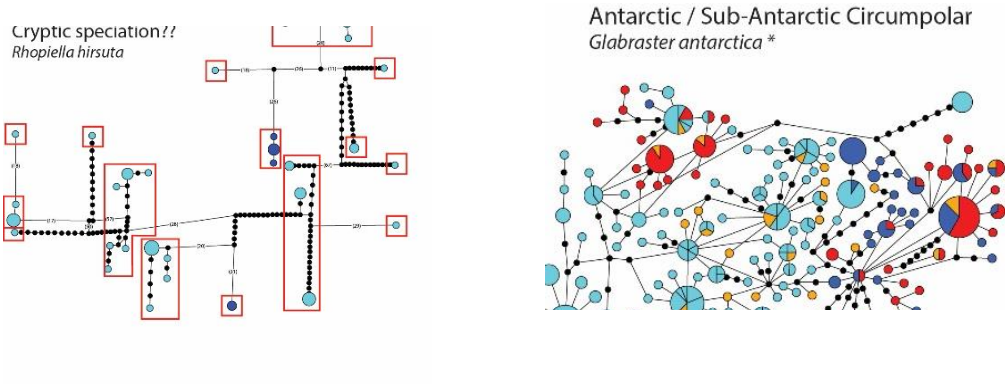


Figure 3 a & b: COI haplotype networks of two sea star morphospecies illustrating cryptic diversity. From Moreau et al. (2021).

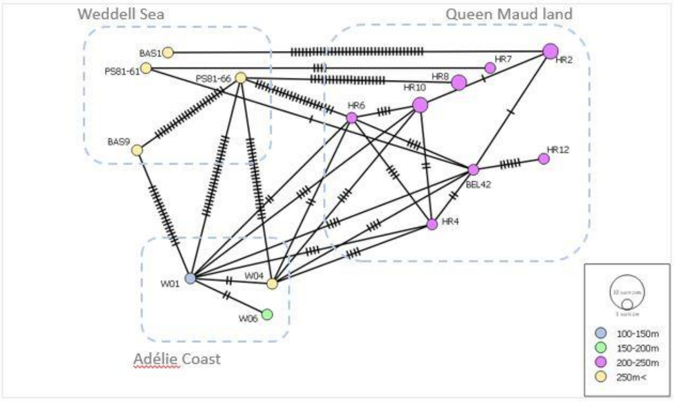


Figure 3c: COI haplotype network of the amphipod morphospecies *Charcotia amundseni* with cryptic species. Cryptic diversity is illustrated by the large numbers of mutational steps between individual haplotypes. (Aerts et al. in prep.).

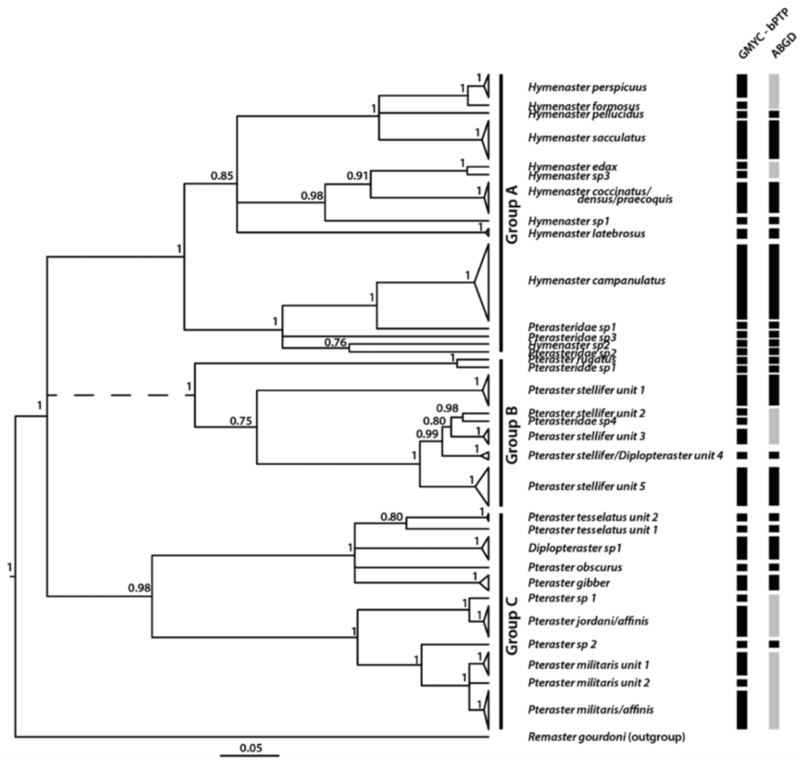


Figure 4. Sea star Bayesian phylogeny based on mitochondrial cytochrome c oxidase subunit I (COI) sequences. Values at each node are the posterior probabilities (nodes with support < 0.75 were collapsed into polytomies). The dashed line (associated with group B) indicates competing topologies from the software denSitree. Assignements for each species delimitation method are reported as black bars [generalized mixed Yule coalescent–Bayesian Poisson tree process (GMYC–bPTP) on the left and automatic barcode gap discovery (ABGD) on the right]. Distinct GMYC–bPTP and ABGD assignements are highlighted by grey bars for the ABGD assignements. From Jossart et al. (2020).

Interestingly, several species were shared between the Northern and Southern Hemisphere (e.g. *Pteraster jordani/affinis*) raising new questions on how these evolved and speciated. Jossart et al. (2020) confirmed the taxonomic status of certain sea star groups while the taxonomy of others will need to be re-evaluated at both genus and species levels in future research.

Besides DNA barcoding, the assembly of complete mitogenomes proved to be an excellent novel molecular tool. For sea stars, for example, 16 new, complete mitogenomes were assembled which will help to solve long-standing questions of sea star evolution and taxonomy (see above, Figure 4 on sea star phylogeny). The novel mitogenomes of three Antarctic amphipod species show a high number of changes in mitochondrial gene orders as compared to the pancrustean pattern and also to other amphipod mitogenomes (Salabao et al. 2022), a pattern which is similar to the results of a new study on Antarctic fish (Papetti et al. 2021). In contrast, we did not find changes of mitochondrial gene order in different populations *Laternula elliptica* (Cordone et al. in prep.) or the newly assembled mitogenome of Aquiyoldia (Duncan et al. in prep.) which has the same gene order as other bivalves. On the whole, the generated mitogenomes have shown to provide about 15,000 basepairs of data each, much more than the 700-800 basepairs commonly generated during classic DNA barcoding, and thus can facilitate phylogenetic and phylogeographic reconstructions with better statistical support. This approach can therefore be highly recommended for future work especially when it can be conducted in a cost-efficient way as detailed in Hinsinger et al. (2015) and employed at the sub-contractor MNHM. Furthermore, mitogenomes can provide additional insights into cold adaptations (e.g. Li et al. 2019) which are of high relevance for the evolution of Antarctic taxa. This hypothesis is currently tested for amphipod mitogenomes (Salabao et al. in prep.).

4.3 Reconstruction of post-glacial refugia, population histories and population connectivity

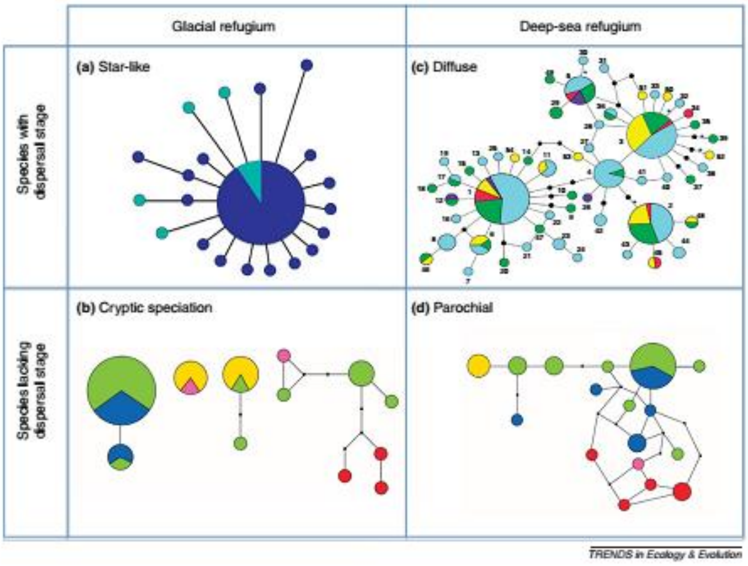
The optimized RRS protocols (Christiansen et al. 2021) was meanwhile already successfully applied to sea stars and bivalves (see next paragraphs). These protocols will be extremely useful for the Antarctic research community and beyond as the different optimization steps of Christiansen et al. (2021) can easily be applied to other organisms. Because of too variable and possibly huge genome sizes, amphipods could also not be included in the test sequencing runs for the final optimization; for them, other molecular approaches have been proposed (Christiansen et al. 2021) until exact estimates of genome sizes will become available for this crustacean group as they are foreseen in the BRAIN project COPE, which started in 2020. Applying the optimized protocol produced inadequate sequencing results for the snow petrel samples, probably because of degenerated DNA due to non-invasive sampling. Microsatellites (see below) or other protocols for DNA extractions will need to be further developed for these birds in the future. It is the first time that such an optimization of RSS protocols was successfully achieved for such a wide taxonomic range of animals in general and for Antarctic animal in particular.

4.3.1 Snow petrels representing top predators in the RECTO project

Pagodroma nivea seemed to have colonized Dronning Maud Land more than 37,000 years ago (Thor & Low 2011), before the last glacial maximum. The inland snow petrel population in the Sør Rondane Mountains in Eastern Dronning Maud Land in the vicinity of the Belgian Princess Elisabeth Station was much larger than previously expected and comprised in 2017-2018 more than 2000 breeding pairs in 16 breeding colonies (Robert et al. in prep.).

Analysing DNA sequence data from three different mitochondrial genes (16S, Cytochrome B and COI; bachelor thesis of Phadra Oels) of snow petrels indicated connectivity between all breeding colonies of the Sør Rondane Mountains. Including additional sequence data from other localities and from GenBank showed that the Sør Rondane Mountains populations are most likely genetically also connected to populations elsewhere on the Antarctic continent (Larsemann Hills and Schirmacher Oasis in Central Dronning Maud Land, Robertkollen, Storm Ridge), to Rothera at the West Antarctic Peninsula and also to South Georgia as no genetic population structure could be detected. In contrast to the predictions of Jouventin & Viot (1985), we thus did not find any evidence for the existence of two *Pagodroma nivea* subspecies in the analysed populations, which could reflect different postglacial refugia. Our results matched those of Carrea et al. (2019) who analysed several mitochondrial genes and one nuclear gene and also did not find any geographic patterns. Since the lack of any phylogeographic structure might be explained by a too slow molecular evolution of mitochondrial markers, we also screened the microsatellites of Pande et al. (2018) for snow petrel samples of the RECTO project. The preliminary results of the master thesis by Manon Bayat (ULB) indicated that snow petrel populations from Adelaide and Signy Island were highly connected and could possibly form one panmictic population but the data were derived from small sample sizes. These populations also showed genetic connectivity to the population of the Sør Rondane mountains albeit with some (low) genetic differentiation. The snow petrel colonies in Sør Rondane had a high connectivity between each other and should genetically be considered as one population, similarly to the results from the mitochondrial markers. The lack of any clear genetic structure can most likely be explained by the large distances that snow petrels migrate away from their colonies when they are not breeding (Delord et al. 2016; Quillfeldt et al. 2017). These promising preliminary results need to be further confirmed in the future because of the low samples size (owing to non-invasive sampling) and the possible presence of null alleles as microsatellites were developed for other petrel species and not specifically for the snow petrel (Pande et al. 2018).

4.3.2-4.3.5 Sea stars, amphipods and bivalves representing Antarctic benthic organisms



TRENDS in Ecology & Evolution

Figure 5: Shapes of mitochondrial haplotype networks illustrating the effects of different glacial refugia and dispersal capacities on genetic structures. (From Allcock & Strugnell 2012).

RECTO had set out to use molecular data for the reconstruction of past refugia and population histories focusing on haplotype network analyses from mitochondrial data as the scenarios of Allcock & Strugnell (2012) could be applied (Figure 5). This aim could be achieved for all target animals except ostracods where the sample numbers per site were too low for population genetic analyses. For the bivalve *Aequiyoldia eightsii* and the sea star *Bathybiaster loripes*, the optimized protocol for population genomic analyses (Christiansen et al. 2021) which was developed during RECTO could already be successfully applied (Jossart et al. in prep.; Van Cranenbroeck et al. in prep.); for *Trematomus* fish and amphipods, this kind of techniques is currently used in the subsequent BRAIN project COPE (Christiansen et al. in prep.; Aerts et al. in prep.).

For sea stars, different phylogeographic patterns were observed in the constructed haplotype networks (Moreau et al. 2019, 2021): in *Rhopiella hirsute and Chiraster sp.*, cryptic diversity was found, resembling pattern 1b of Figure 5 and indicating glacial refugia. In contrast, the haplotype network of *Glabraster antarctica* had a diffuse structure indicating deep sea refugia (Moreau et al. 2019). Two *Bathybiaster* species (Figure 6) showed different population histories with *B. loripes* having recolonized the Southern Ocean from the Deep Sea and *B. vexillifer* from the Antarctic Shelf and the Sub-Antarctic Kerguelen and Magellanic areas (Moreau et al. 2019, 2021; Fig. 6).

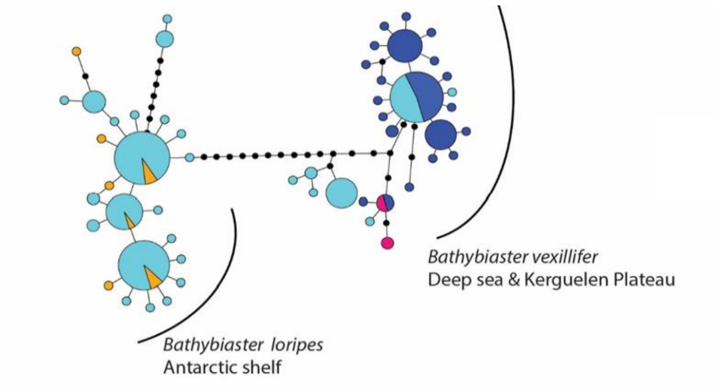


Figure 6: Haplotype network of two *Bathybiaster* sea star species. Circles indicate individual haplotypes while the size of the circle represents the number of sequences of this particular haplotype. Small circles between haplotypes indicate mutational steps. Different regions are indicated by different colours in the pie charts; the portions of the pie chart are proportional to the number of sequences from that particular region. Light blue – Antarctica ; orange – South Georgia ; dark blue – Sub-Antarctic Kerguelen ; red – Subantarctic – Magellanic. From Moreau et al. (2019, 2021).

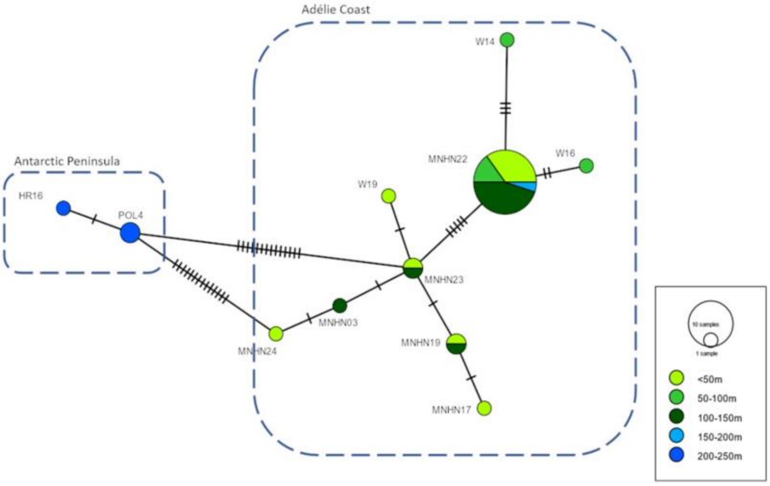


Figure 7: Haplotype network of the amphipod *Charcotia obesa* based on mitochondrial cox1 sequences. Circles indicate individual haplotypes while the size of the circle represents the number of sequences of this particular haplotype. Lines between haplotypes indicate a single mutational step, horizontal lines multiple mutational steps. Different depths are indicated by different colours in the pie charts; the portions of the pie chart are proportional to the number of sequences from that particular depth. Dashed blue lines represent the regions which were sampled. (Masterthesis Tim Plevoets).

The phylogeography and population history of the amphipod genus *Charcotia* (formerly known as *Waldeckia*) was investigated for two species: *C. obesa* and *C. amundseni*. *Charcotia obesa* showed differentiation between samples sites and depths, with the occurrence of a star-like structure in the network. This is a typical network structure for populations with a history of bottleneck events (Fig. 7) and indicates glacial refugia (scenario a in Figure 5) despite the fact that these amphipods do not have larval dispersal (Aerts et al. in prep.). *Charcotia amundseni* exhibited no dominantly occurring haplotype but showed multiple haplotypes with varying degrees of differentiation (Figure 8). This pattern resembles a parochial haplotype network, which can be found in organisms that used the deep-sea as refugia (scenario d of Fig. 5). Additionally, species delimitation analysis indicated the possible presence of multiple cryptic species, although further morphological confirmation will be necessary (Aerts et al. in prep.). Restricted gene flow and the presence of multiple genetic species could limit the recovery potential to climate change-induced environmental disturbances. This example furthermore showed that population histories of closely related species can be very different, similar to the two sister species of the sea star genus *Bathybiaster* (see above).

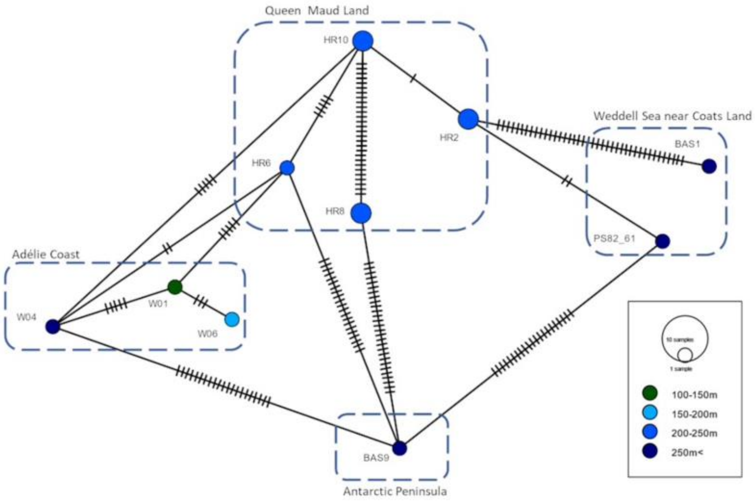


Figure 8: Haplotype network of the amphipod *Charcotia amundseni* based on mitochondrial cox1 sequences. Circles indicate individual haplotypes while the size of the circle represents the number of sequences of this particular haplotype. Lines between haplotypes indicate a single mutational step, horizontal lines multiple mutational steps. Different depths are indicated by different colours. Dashed blue lines represent the regions, which were sampled. (Masterthesis Tim Plevoets).

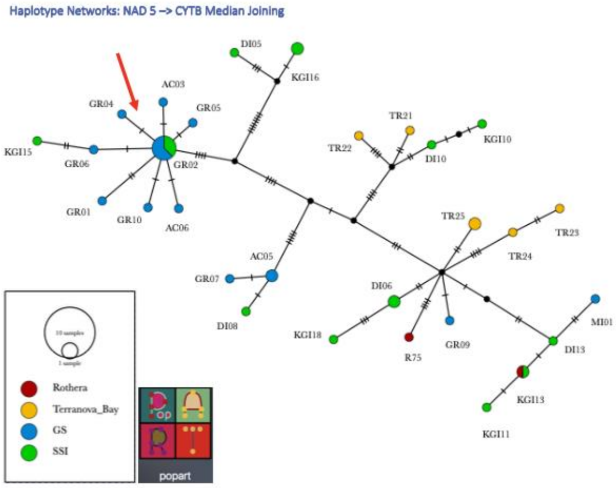


Figure 9: Median-joining haplotype network of the bivalve *Laternula elliptica* reconstructed from two mitochondrial genes. (Cariolata et al. in prep.).

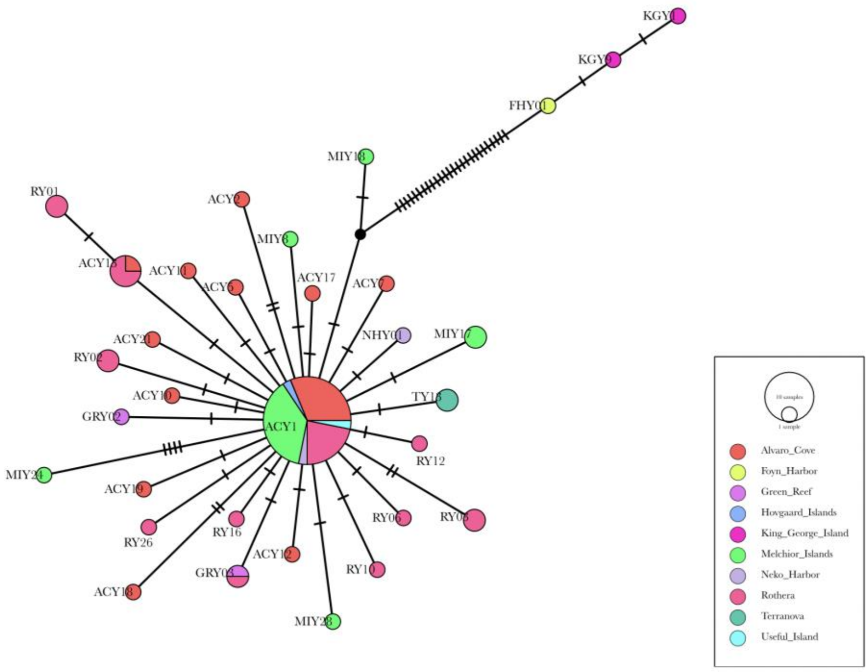


Figure 10: Median-joining haplotype network of *Aequiyoldia eightsii* reconstructed with parts of the mitochondrial genome. (*Cytb, COX2, tRNA-Q, tRNA-S2, tRNA-W, tRNA-A, tRNA-L2, tRNA-R*, and *tRNA-V genes*; Dukan et al. in prep.).

All haplotype networks of *Aequiyoldia eightsii* showed a star-like pattern (see Figure 10 for an example; Dukan et al. In prep.), which indicated haplotype diversity loss and a former bottleneck in population size. Such a bottle neck event could be correlated to the last glacial maximum. Star-like haplotype network patterns are indicative of glacial refugia (scenario a in Fig. 5) or continental-shelf refugia.

The RRS protocol was successfully applied to the bivalve *A. eightsii* during the MSc thesis of Lore Van Craenenbroeck and allowed us to analyze thousands of Single Nucleotide Polymorphisms to study population connectivity and structure.

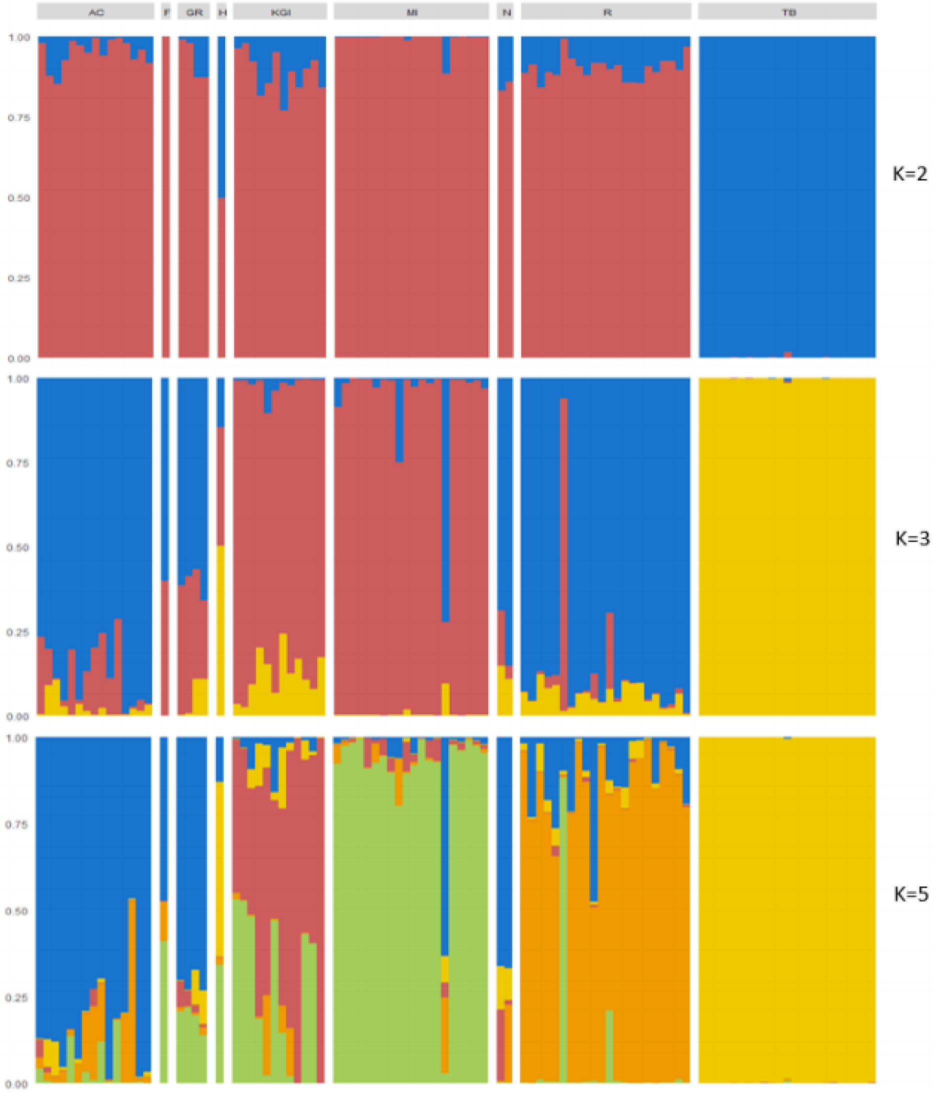


Figure 11: Barplots from the STRUCTURE program for different values of K (=number of genetic clusters) in the bivalve *A. eightsii*. Individual bars in the plots represent different bivalve individuals, while the colours of the bars specify the membership probability to different genetic clusters. Abbreviations: Alvaro Cove (AC), Foyn Harbour (F), Green Reef (GR), Hovgaard Island (H), King George Island (KGI), Melchior Islands (MI), Neko Harbour (N), Rothera (R), Terra Nova Bay (TB). Van Craenenbroeck et al. (in prep.).

Similar to other taxa as for example sea stars and ice fish, we found two major genetic groups of *A. eightsii* separating East Antarctica from populations of the Western Antarctic Peninsula (WAP) (Fig. 11). The high genetic differentiation between these populations might be driven by the large geographical distance (> 5000 km) that separates them, which might be difficult for bivalve larvae to bridge. There were also several genetic subgroups of the WAP, which could be caused by local oceanographic features like ocean currents allowing or restricting gene flow between the different locations. For reconstructing population history, we generated a stairway plot, which indicated a bottleneck occurring in the Terry Nova Bay population about 20 000k years before present, matching the results from the mitochondrial haplotype networks (see above). Which factors could have possibly caused such a bottle neck are currently further examined to prepare these results for publication.

In summary, the RECTO project found different scenarios of post-glacial refugia and population histories for the investigated animal groups. Snow petrels did not show any population structure at the local level in the Sør Rondane Mountains and also little genetic differentiation to other populations, which could possibly have been expected because of their high mobility but defeats results of older studies suggesting two subspecies of snow petrels because of two different refugia. The population structure of this bird species at a larger scale still needs to be further investigated as sample numbers were too limited to draw final conclusions.

For invertebrates, RECTO found evidence for refugia in the deep sea, glacial refugia, and refugia on the continental shelf and in Sub-Antarctic regions. The phylogeographic patterns of the amphipod *C. amundseni* (Fig. 8) as well as the bivalve *Laternula elliptica* (Fig. 9) were indicative for at least two types of glacial refugia. Lau et al. (2020) mentioned in their review the possibility of multiple glacial refugia for marine Antarctic organisms, and this should certainly be further investigated in the future as the patterns of previously published molecular data did not match past ice-free areas from ice core data (Lau et al. 2020).

The phylogeographic results for invertebrates imply that different organisms will have different potential to recover from fast climate change in the future. Some species showed patterns of recent population expansions (the two bivalve species *L. elliptica* and *A. eightsii* as well as the amphipod *C. obesa*) most likely from bottleneck events in the past; it could therefore be expected that their populations will continue to expand although this will need to be further investigated, especially under climate change. On the other hand, species with high cryptic diversities (such as the sea stars *Rhopiella* hirsuta and *Cheiraster sp*. and the amphipod *C. amundseni*) might be more prone to extinction events in the future because of localized genetic diversity and local adaptations to specific abiotic factors, which could reduce the adaptability of these species to fast global warming.

4.5 Macroecology and evolutionary ecology

4.5.1 Trophic ecology of fish, snow petrels, sea stars and of fish, snow petrels

As a newly developed part of the RECTO project, the KU Leuven team applied barcoding to study the diet and microbiome of Trematomid fish from recent and historic samples (Heindler et al. 2018). Although historic samples had a limited success rate for this molecular study, it was still possible to detect shifts in the microbiome of this Antarctic fish within 100 years. The metabarcoding approach of recent samples was highly successful to identify the diets of different species, which will be of very high relevance for future ecological studies.

For ice fishes, the objectives of our morphological analyses on different trophic traits (e.g. head shape, morphology of appendices…) were two-fold. Firstly, we aimed to extend the time frame of our study on trophic differentiation because variation in trophic niche breath or trophic specialization can result from varying opportunism or patchily distributed preys (Bolnick et al. 2003). Secondly, the quantification of morphological diversity within the studied taxa provided the raw data to compare patterns of morphological evolution (see hereafter 4.5.2).

By combining isotopic and morphological data collected from the same specimens, we aimed to test ecomorphological hypotheses and to define trophically relevant morphological traits in Antarctic fishes and amphipods. Through a sample of 14 cryonotothenioid species spanning three different families, we revealed that ^{15}N values are positively related to fish body size ($r^2 = 0.22$, p-value = $7.2\text{x}10^{-8}$). On the other hand, we found poor relationships between the morphology of gill rakers, eye size, head shape and isotopic data. These analyses show that the morphological diversity of Antarctic fishes is so disparate among major lineages that it may obscure ecomorphological relationships. On the other hand, our results ask for additional works with similar approaches at the family levels.

The isotopic niches of juvenile snow petrels were similar to each other indicating that parents feed their young with prey from the same part of the Southern Ocean and with similar prey (Master thesis of Jonathan Baricalla 2021). In contract, the isotopic niches of adult snow petrels were more variable. This suggested that there were individual differences because of other overwintering areas and/or other prey. The latter results would need to be further confirmed, for example with tracking data. No correlation between mercury contamination and isotropic niches was found although juveniles had less mercury concentration than adult snow petrels. Comparing the stable isotope results of snow petrels close to the PES (Bachelor thesis Yelle Vanboer 2019) to other studies indicated a decreasing level of the proportion of consumed high trophic level prey. A similar comparison to other Antarctic seabird species showed that snow petrels at Princess Elisabeth station had an intermediate position and snow petrels from the Western Antarctic Peninsula had the smallest proportion of consumed prey from high trophic levels

In order to better understand the potential importance of sea stars in the ecosystems of the Southern Ocean, the food web of subantarctic *Macrocystis pyrifera* (Phaeophyceae, Laminariales; or “kelp”) forests from Kerguelen Island was reconstructed by analysing stable isotope values in invertebrates (19 taxa, including 6 sea star taxa) and primary producer tissues (Figure 12). Mixing models did not indicate major *Macrocystis pyrifera* consumers and showed that the food web was supported by pelagic organic matter and living (with the exception of kelp) or detrital micro/macrophytobenthos. This suggested that sea stars did not have the same ecological function in *Macrocystis pyrifera* forests from Subantarctic regions as those from more temperate regions, where they control grazer populations. The results also showed that sea stars were not only top predators in the food chain. Some species might occupy lower trophic positions, but their trophic niches might not overlap: some species relied more on the food chain being supported by pelagic production and others on the food chain being supported by benthic (including detrital) production.

The impact of trophic group, depth, sea ice concentration and the season duration of sea ice on the trophic ecology of sea stars was assessed by a global analysis of the seastar dataset at the scale of the entire SO. The SO was subdivided into different benthic ecoregions according to environmental (seabed temperature, sea ice, bathymetry) and biotic data (species distribution), to study biogeographic variations in the trophic ecology of sea stars. This subdivision notably highlighted the separation between Antarctic and Subantarctic environments, with the different δ^{13}C values in organic matter from the surface in Subantarctic and Antarctic waters being reflected in tissues from benthic sea stars. The compilation of the available information on their diet allowed to classify sea star taxa from the SO into trophic groups, ranging from suspension feeders to predators of active prey. The differences of stable isotope values between trophic groups and their variability suggested a diversity of food sources and/or of feeding strategies between and within trophic groups. These results confirmed that, contrary to what was sometimes stated in the literature, sea stars in the SO showed a great trophic diversity. Depth had important effects on the trophic ecology of sea stars, both across the entire SO (Fig. 13) and within ecoregions (PhD thesis of Baptiste Le Bourg). Indeed, coastal sea stars might exploit food webs supported by a variety of pelagic and benthic primary producers while sea stars occurring at greater depths might depend on the sedimentation of the surface primary production. Coastal sea stars were consequently characterised by a high diversity of food sources, while sea stars from deeper waters had a higher diversity of trophic positions as compared to coastal ones.

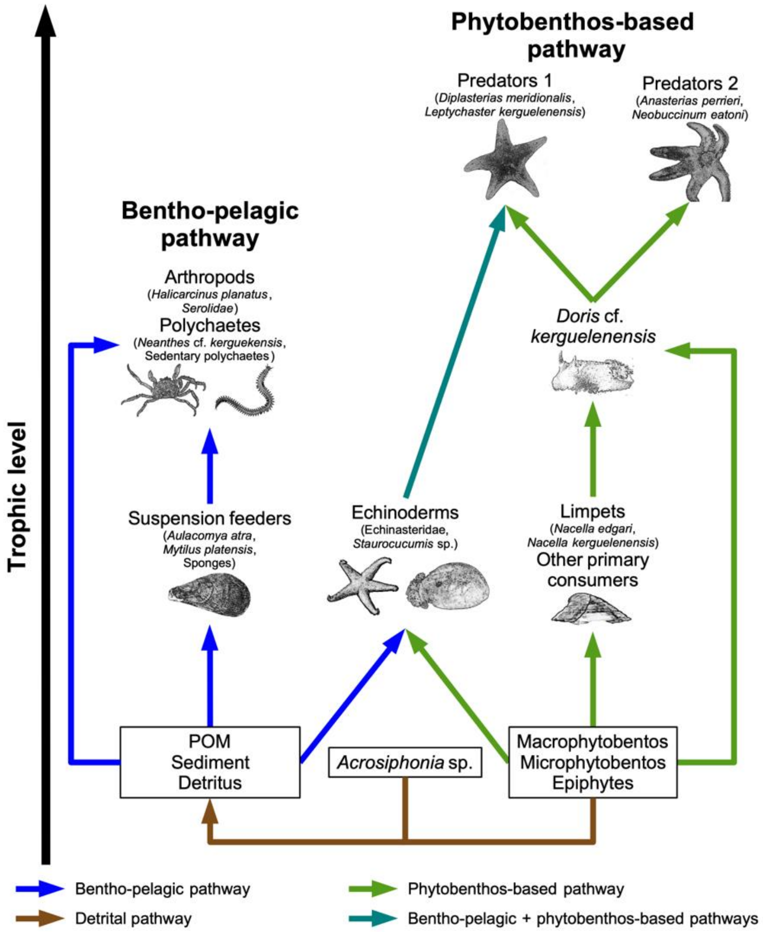


Figure 12: Conceptual food web of the shallow subtidal benthic community of Kerguelen Islands. Each arrow indicates a carbon transfer between two organism groups. Full arrows indicate trophic transfers highlighted by the mixing models using stable isotope data (Le Bourg et al. 2022).

The impact of sea ice on the trophic ecology of sea stars was also investigated. The sympagic communities might be used as a food source by sea stars in case of high sea ice concentrations and in shallow areas (Fig. 14). The impacts of the environmental parameters might differ between trophic groups, indicating the importance of trophic diversity to predict the sensitivity of sea stars to future environmental changes, whether natural or anthropogenic. To summarise, our study showed that the trophic ecology of sea stars from the SO was impacted by a combination of intrinsic (body size, trophic group) and extrinsic features (turbidity, depth, sea ice). Information on the influence of environmental parameters might provide hypotheses regarding the possible impacts of climate change on sea stars and on their role in benthic food webs of the SO.

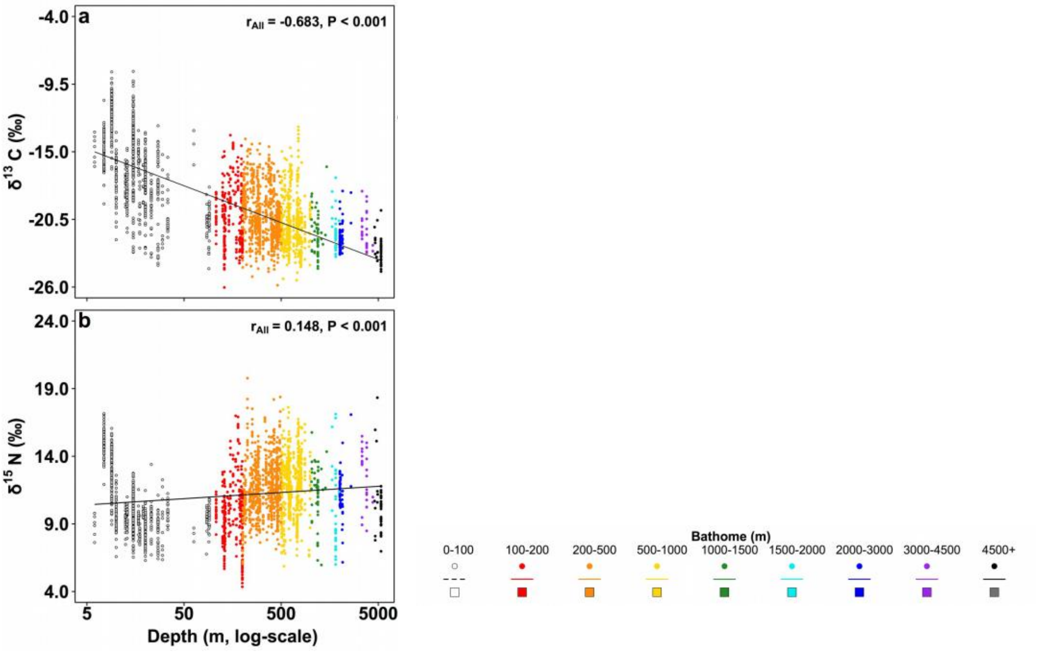


Figure 13: Effect of depth on sea star δ13C and δ15N values: relationships between depth and a) δ13C and b) δ15N values. (n = 2658 individuals).

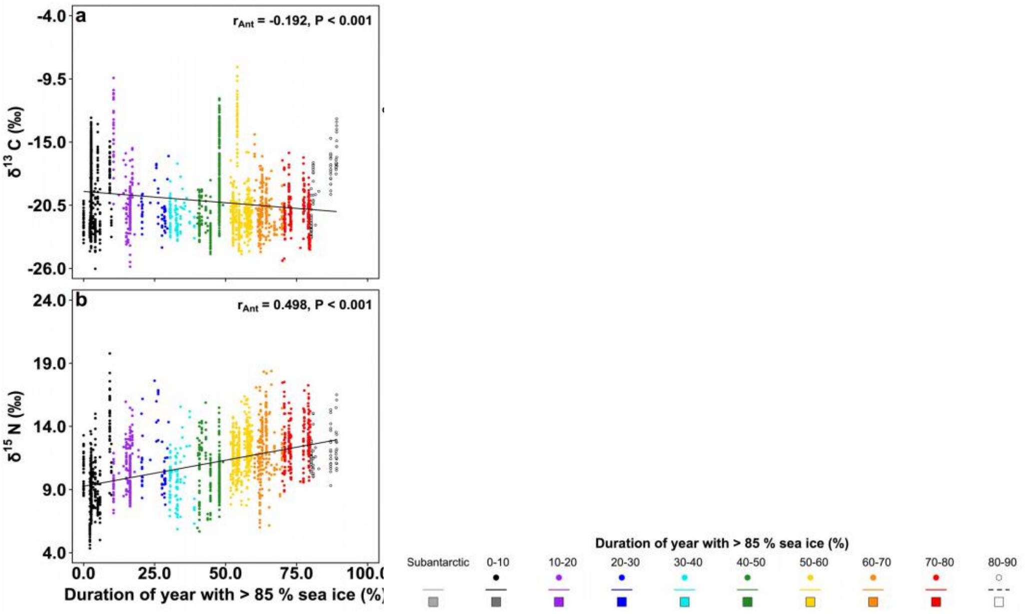


Figure 14: Effect of sea ice season duration on sea star δ13C and δ15N values: relationship of sea ice season duration with a) δ13C values and b) δ15N values in Antarctic sea stars.

4.5.2 Patterns of morphological and evolutionary diversification

We aimed to study the evolutionary history of two taxonomic groups for which phylogenetic hypotheses were already available: the cryonotothenioid fishes as well as *Eusirus*, *Epimeria* and Iphimediidae amphipods. These tasks involved the combination of morphological, ecological, isotopic, and phylogenetic data sets.

We were able to decipher the patterns of morphological and ecological diversification in Antarctic fishes through ongoing collaborations of ULiege with the University of Yale and the University of North Carolina testing the effects of past climatic changes on the current Antarctic fish diversity and ongoing trajectories of morphological evolution. High trait disparity (body shape, buoyancy) was observed among closely related species of notoperches (Trematominae) and crocodile icefishes (Channichthyidae) (Parker et al. in press). These results supported the hypothesis that periodic climate change in Antarctica's SO had catalyzed continual repetition of the early stages of adaptive radiation in notothenioids. This signature of repeated morphological convergence was demonstrated at both the interspecific (macroevolutionary level) and the intraspecific level (microevolutionary level) in Trematominae. Phenotypic plasticity characterized various species of Trematominae and intraspecific variability was described in many *Trematomus* species. For example, plasticity was well documented in *T. newnesi* with least two ecomorphs, i.e. typical and large-mouth morphs (Eastman & DeVries 1997; Piacentino & Barrera-Oro 2009). We tested whether the level and the main axes of shape variation differed between the macro- and microevolutionary level. A visual exploration of the distribution of fish specimens in the shape space (Principal Component analyses of shape variables) showed overlaps between species and illustrated extensive shape variation within species (Fig. 15) (Frederich et al. 2022). The level of morphological variation within *T. hansoni*, *T. newnesi* and *T. bernacchii* was high and accounted for a large proportion of the *Trematomus* head shape disparity. This was further confirmed by calculating shape disparity levels based on Procrustes variance. For example, the level of shape disparity for all *Trematomus* did not differ significantly from those of *T. bernacchii* and *T. hansoni* ($P > 0.06$). In addition to the similarity in the extent of shape disparity, the major axes of shape variation were shared at the macro- and micro-evolutionary level. Taken together, the study by Frederich et al. (2022) showed that the morphological diversity of Antarctic fish resulted from repeated events of adaptive radiation following periods of climatic disturbance. The morphological and the ecological variation observed at species levels suggested ongoing processes of diversification and potential reservoirs of adaptation.

Applying an integrative approach of cutting-edge phylogenetic, stable isotope and morphometric to iphimiid amphipods (Verheye et al. in prep.; Fig. 16) provided preliminary evidence for the absence of an early burst of lineage diversification; later bursts (appr. 7-3 Mya) in two subclades were found, which could result from the invasion of novel ecological niches or from Pleistocene glacial cycles, which were hypothesized to act as diversity pumps.

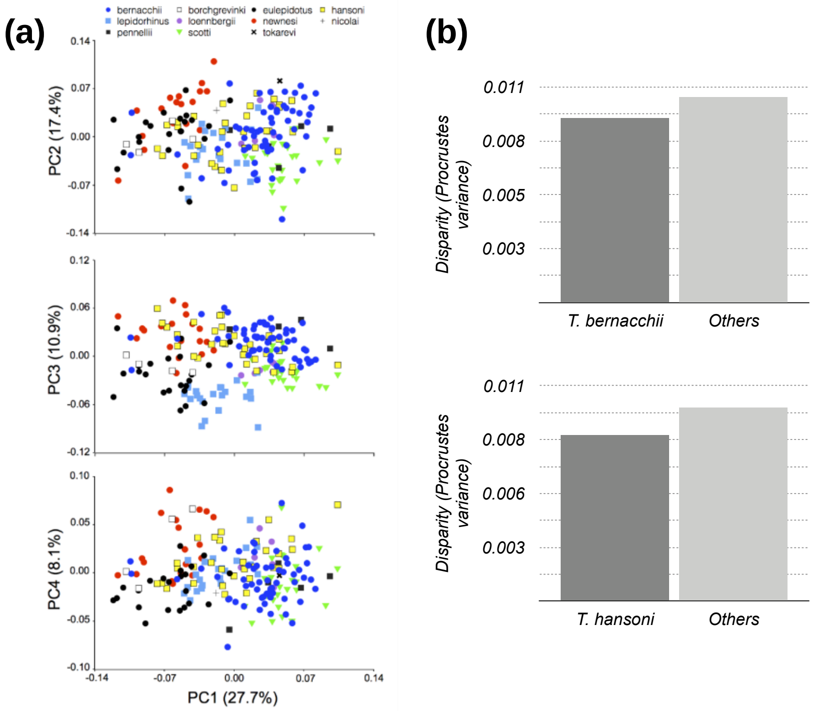


Figure 15: (a) Ordination of 11 *Trematomus* species in the shape space defined by the first four principal component axes (PC1-PC4) based on shape data. Species are indicated by different symbols and colors. Percentage of shape variance summarized by each PC is given in parentheses; **(b) Comparisons of the head shape disparity levels between *T.hansoni*, *bernacchii* and the pool of other *Trematomus* species.**

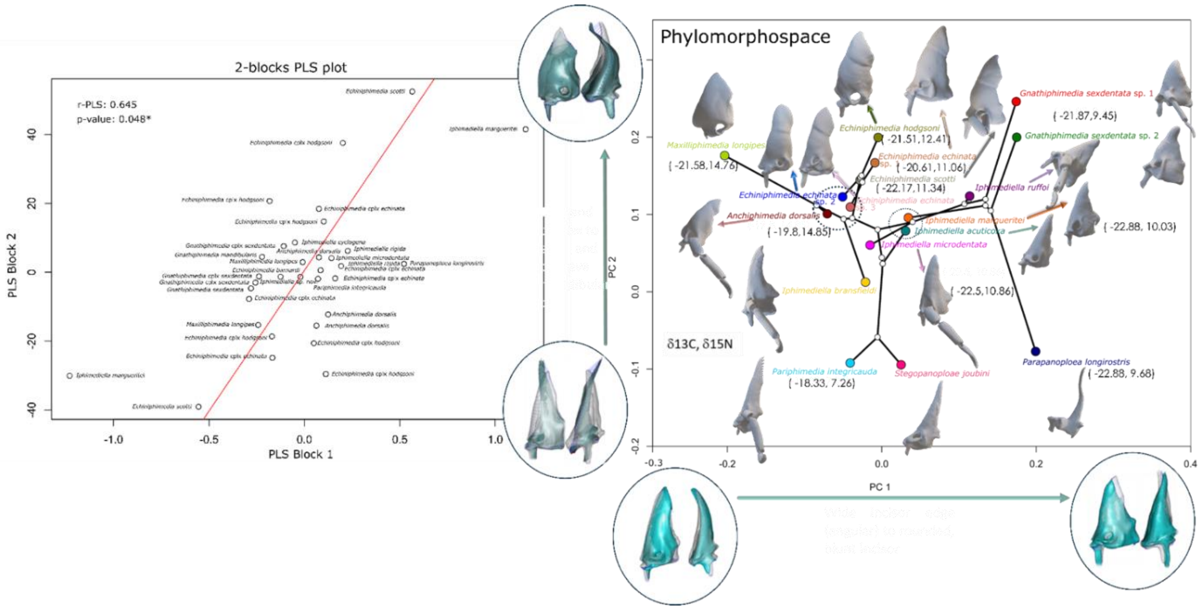


Figure 16: Two-blocks PLS illustrating the relationship between isotopic data and mandible shapes (left) and phylomorphospace showing mandible shape variation across amphipods from the family Iphimediidae (right).

4.4.2 Physiology

Field experiment

Recorded acid-base characteristics of both studied species fitted the general picture deduced from temperate and tropical sea stars and sea urchins but conditions and possibly confounding factors, principally food availability and quality, in the studied stations prevented definitive conclusions. Reduced seawater pH 7.8 and metals had almost no impact on the skeleton mechanical properties of the two investigated species despite very high Cd concentrations in *O. validus* integument. Reduced pH was correlated to increased contamination by most metals, but this relation was weak.

Aquarium experiment on O.validus

Provided food was poorer than what the individuals experimented in their original environment. Proximal data showed a decrease in weight in all treatments, larger in non-feeding individuals and at higher temperatures. Metabolic rate increased with temperature, however, by the second year, metabolic rate was compensated and not significantly different between temperatures. Gonad histology showed that gamete development was normal, and experimental individuals spawned in the aquaria during the first year and again during the second year. However, gonad index indicated a poor gonad growth between spawning events in all treatments. Sampling after two years occurred after the natural spawning season; therefore, the number of females capable of spawning was small. Still, cultures and egg samplings for biochemistry were started from all temperature treatments. No apparent effect of pH was found on proximal data or metabolic rate. Carbon chemistry of the coelomic fluid was different at different pH_T treatments, with coelomic fluid pH_T being consistently ~0.3 below treatments pH_T. Total alkalinity of the coelomic fluid was not significantly different from seawater. These patterns did not change after 12 months of exposure. Results on egg biochemistry and larval rearing are still pending. The same applies to results on skeleton biomechanics.

Aquarium experiment on A.cordatus

Up to the 4th day after reaching the target pH, the coelomic fluid pH_T (pH_{CF}) decreased parallel to that of sea water. However, after 8 days, the pH_{CF} increased with a full compensation for sea urchins at pH 8.0 and a partial one for sea urchins at pH 7.7 and 7.4. Surprisingly, this is apparently not due to an accumulation of bicarbonate ions as observed in regular sea urchins which are compensating their pH_{CF}. The pH_T of the sea water enclosed in the brooding pouches was also monitored. It varied parallel with that of sea water, being 0.2 to 0.4 units below the latter. This indicated that juveniles developing in the pouches were submitted to a worse acidification than that of sea water. These juveniles were probably much more at risk than adults**.** In few of global change where ocean acidification is one of the risks for the SO, it can thus be expected that juvenile sea urchins could be more affected than adults.

4.4.3 Ecological modelling

For fundamental niche modeling using Dynamic Energy Budget (DEB) theory, one of our studies (Guillaumot et al. 2020b) used the limpet species *Nacella concinna* (Strebel, 1908), which is known to have distinct intertidal and subtidal morphotypes that are genetically similar but differ in morphology and physiology. This species was used as a case study to (1) evaluate the potential of the DEB approach and assess whether a DEB model could be built separately for the intertidal and subtidal morphotypes, based on a field experiment and on data from the literature and (2) analyze whether models were sufficiently contrasting to reflect the two morphotypes' respective physiology and morphology. A second study (Arnould-Petré et al. 2020) focused on population dynamics modelling. Using an Individual Based Modelling approach (IBM), DEB models can be upscaled to the population level to simulate the response of populations to variations in food resources and temperatures. The DEB-IBM approach was applied to an endemic sea urchin of the Kerguelen Plateau, *Abatus cordatus* (Verrill, 1876) and modelled population changes through time, according to changes in food and temperature conditions, for present and future temperature scenarios. Finally, DEB modelling was applied to better understand the role of low temperature and seasonal food availability conditions on the life cycle and reproduction strategy of an Antarctic bivalve, *Laternula elliptica* (King, 1832) (Agüera et al. 2017). The DEB model was also used to describe the effect of varying environmental conditions on energy allocation, using an available time-series dataset.

The potential, limits and methodological issues of Species Distribution Models (SDMs) applied to the SO were also addressed for a series of benthic case studies on species realized niche. We first reviewed these SO dataset peculiarities, highlighted the main methodological limits to SDMs applied to SO case studies and provided some new methods (from the studies below) to generate more accurate models (Guillaumot et al. 2022). We also progressed on model evaluation by proposing cross-validation procedures which aim at splitting occurrence datasets into training and test subsets (Guillaumot et al. 2022). However, SO occurrence datasets are often spatially aggregated, which violates independency between training and test subsets and biases the accuracy of model evaluation. We compared several cross-validation procedures (random vs. spatial partition of training-test subsets) for the case study of the sea star *Odontaster validus* Koehler 1906 (Agüera et al. 2015). In another study, six sea star species having a circumpolar distribution were used as case studies to generate SDMs with contrasting numbers of environmental descriptors (Guillaumot et al. 2020b). The influence of the number of these environmental predictors and of the collinearity between them was assessed. We then focused on extrapolation uncertainty in SDM predictions (Guillaumot et al. 2020b). Considering the reference dataset of environmental conditions for which species presence records are modelled, extrapolation corresponds to the part of the projection area for which at least one environmental value falls outside of the reference dataset. Due to the vast extent of the SO and data gaps in occurrence datasets, extrapolation represents an important part of model predictions. Using the case study of six sea stars species, extrapolation was highlighted and methods were provided to improve model predictions. We finally analyzed the influence of spatial and temporal aggregation of occurrence datasets on modelling performances (Guillaumot et al. 2018). The case studies of four sea urchin species found on the Kerguelen Plateau were analyzed. Methods to correct for the effect of spatial sampling bias were applied and proved their efficiency to generate more accurate predictions.

As proposed in the RECTO project application, we also attempted a range of integrated modelling approaches. Coupling SDM predictions with experimental results, in situ observations or results from other modelling approaches that detail species physiological tolerance, migratory potential or biotic interactions was shown to improve the relevance of species niche estimation. Such methods have however been rarely applied to SO marine case studies. We also investigated the integration of SDMs with physiological information in three studies. The first (Lopez-Farran et al. 2021) assessed the potential of the Patagonian crab *Halicarcinus planatus* (Fabricius, 1775) to survive in the Western Antarctic Peninsula using two approaches: experimental data that characterized the physiological boundaries of larvae and adult to temperature and salinities and SDMs that simulated species occupied space in present and future environmental conditions. In the second analysis (Fabri-Ruiz et al. in press), we used data on the sea urchin *Sterechinus neumayeri* (Meissner, 1900) to compare DEB model spatial projections and SDM predictions. Comparisons were performed for contrasting environmental conditions and future simulations. In a third analysis, we used data from a long-term observation network located in the Kerguelen Islands, to implement the first SO integration of DEB and SDM models to predict the distribution of an endemic sub-Antarctic sea urchin, *Abatus cordatus* (Verrill, 1876) as a response to environmental drivers (Guillaumot et al. 2022). We compared the performance of simple SDMs and integrated approaches to predict the distribution of *A. cordatus* under seasonal variations. Two integrated approaches were studied and performed by either (1) including the spatial projection of the DEB model as an input layer inside the SDM or (2) using a Bayesian inference procedure to use DEB model outputs as priors of the Bayesian SDM. These examples illustrate that the modelling approaches of RECTO are extremely useful tools for the prediction of responses of species from the SO to future global change.

To summarize, results showed that physiological models can be developed for marine SO species to simulate the metabolic variations in link with the environment and predict population dynamics. However, more (experimental) data are necessary to highlight detailed physiological contrasts between populations and to accurately evaluate models. Results obtained for SDMs suggest that models generated at the scale of the SO and future simulations were not relevant, given the lack of data available to quantify the spatial distribution of species, the lack of precision and accuracy of future climate scenarios and the impossibility to evaluate models. Moreover, models extrapolate on a large proportion of the projected area. Adding information on species physiological limits (observations, results from experiments, physiological model outputs) was shown to reduce extrapolation and to improve the capacity of models to estimate the species realized niche. Spatial aggregation of occurrence data, which influenced model predictions and evaluation was also successfully corrected.

We built a novel framework for the future development of ecological models for the SO, including methodological aspects, and annotated codes and tutorials (in open access) to help implement future modelling works applied to Southern Ocean marine species

Ecological modelling has been used intensely during the past two decades to study SO marine species. Modelling is a valuable approach to synthetize diverse information gathered by several scientific teams and during several campaigns. Model maps are handy to interpret, and thus help bridge scientists and the general public, or decision-makers during conservation-related processes. Models are interesting to quickly identify knowledge gaps and set research priorities. They are attractive, as they can integrate different types of data and information and can help recycle left-behind historical data. They are helpful to simplify complex processes, therefore offering the possibility of making preliminary assumptions before further researches are conducted. Finally, within a few months of reading and training, anyone can now generate a model to predict species distribution or model an organism’s metabolism. Modelling is not only accessible to people having a mathematical background. The impressive collection of articles, R packages or tutorials that guide people to create a model, using open source available scripts. All these points can explain the growing popularity of the approach, as experienced in the community of Antarctic biologists.

Keeping the limitations mentioned above in mind, for example, a study on the Kerguelen Plateau region by Saucède et al. (2019) concluded that one echinoderm species was particularly vulnerable to future worst-case climate scenarios due to its narrow ecological niche and endemism to near-shore areas. Likewise, SDMs developed by Guillaumot et al. (2018) for the same geographic region were projected to different time periods, and the magnitude of distribution range shifts was investigated, e.g. under scenario RCP 8.5 for 2050–2099. This study illustrated that species distribution shifts were expected to be more important in a near future. Possible species' responses included poleward shifts, latitudinal distribution reductions, and local extinctions, similar to responses in the past to glacial periods (see above, 4.3). Species with broad ecological niches and not limited by biogeographic barriers were expected be the least affected by environmental changes. In contrast, endemic species being restricted to coastal areas were predicted to be more sensitive.

However, several issues for ecological modelling should be stressed, including:

- It is essential to anticipate the possibility of evaluating model's predictive performance before creating it (Grimm & Berger 2016, Railsback & Grimm 2019). Model evaluation is indeed not always considered with enough importance in SO modelling applications. The evaluation method is often not adapted to the dataset (Guillaumot et al. 2019) or the model not evaluated at all (Griffiths et al. 2017).

- IPCC scenarios are global average scenarios, most of them are not adapted to study species ecology (Cavanagh et al. 2017) and methodological difficulties prevent from incorporating climate scenario uncertainties into model predictions (Freer et al. 2018). Climate scenarios represent the environment with a coarse spatial resolution (100 km) and data on most environmental parameters is not available.

- Generating distribution models at the scale of the entire SO is hardly meaningful, as the quality of environmental and occurrence datasets is not sufficient to precisely distinguish contrasts between species (Guillaumot et al. 2020b). We recommend running models at a regional scale, when datamass is sufficient to describe environmental conditions, and when the relationship between species and their environment (i.e. abiotic conditions, biotic interactions and dispersal abilities) has been scrutinized in terms of species ecological preferences and interactions. Providing uncertainty maps along with model results is also strongly encouraged.

The SO is not as poorly known as often stated (Griffiths 2010). A lot of oceanographic campaigns were undertaken and many datasets are available to modellers. The development of underwater imagery (including habitat modelling) also considerably helps collecting new data. A bit more time is needed before the completeness and quality of datasets can be improved and more accurate models generated. Open-access databases, at the regional scale, could be really helpful for improving modelling studies. Such ideas are progressively being developed by the SCAR community and within Belgian research networks. This would also entail efficient international collaboration and would efficiently support sound conservation decisions.

4.4.4 Oceanic modelling

Passive larval dispersal patterns were successfully simulated with the COHERENS Lagrangian particle mode to contrast these results with other methods as for example genetic or physiological data for several case studies.

For *Chionodraco* fish species, this approach showed that the proposed genetic connectivity between the Antarctic Peninsula and south-eastern Weddell Sea through passive larval dispersal by oceanic currents and passive larval stages was not supported by modelling (Figure 17; Schiavon et al. 2021).

Ballast water exchange has been frequently reported as an introduction avenue in Antarctic waters for alien species. By using a Lagrangian approach, the passive drift of virtual propagules was modelled, which were released in hypothetic ballast water zones and with differing distances from the Western and Eastern coast of the Western Antarctic Peninsula, namely 10, 50 and 200 nautical miles (Duliere et al. 2022). We found that exchanging ballast water at 200 nautical miles reduced the risk of arriving propagules in proposed marine protected areas of the western side of the Antarctic Peninsula considerably. Due to strong currents, propagules can reach marine protected area at the north-easter side of the Western Antarctic Peninsula within a few days regardless of the ballast water zone or its distance to this coast. Our approach also showed that the Patagonian crab (*Halicarcinus planatus*) found in 2010 on Deception Island could have been introduced there through ballast water exchange, if this happened within 50 nautical miles or less from the coast. This illustrates the high potential of this approach for future simulation studies under different climate scenarios. For *Trematomus* fish and bivalves, scenarios are still finalized.

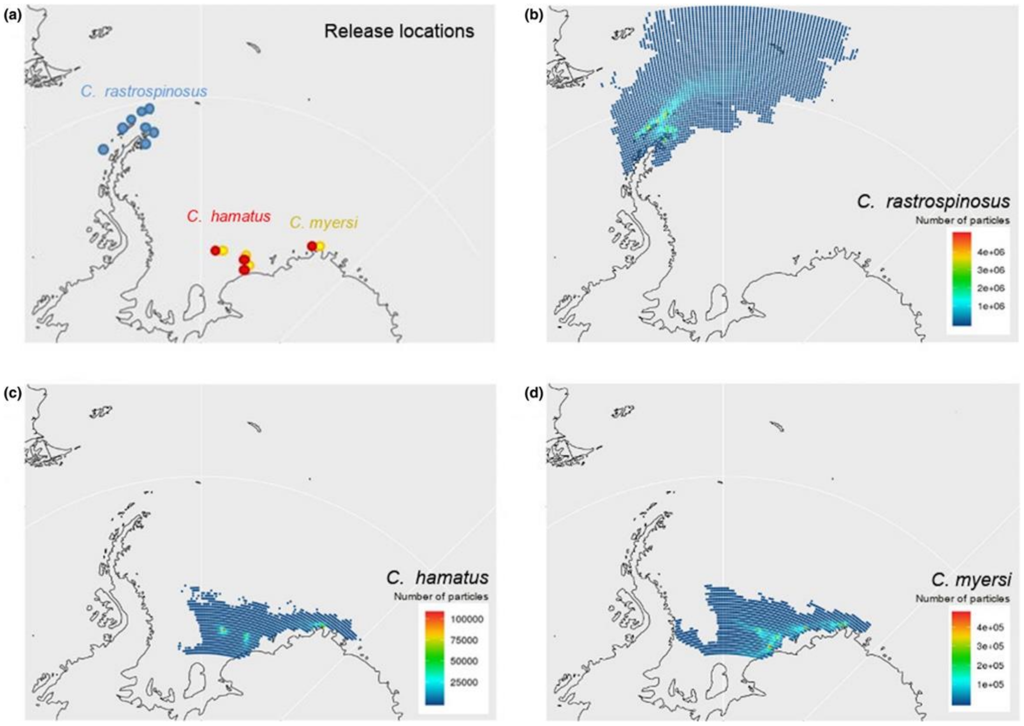


Figure 17: Passive larval dispersal patterns estimated for each *Chionodraco* species and based on Coherens particle module. Panel a: location of spawning grounds from where the passive dispersal phase of the larvae starts (red for *C. hamatus*, yellow for *C. myersi*, blue for *C. rastrospinosus*); panels b, c and d: geographic dispersal patterns of the fish larvae during their pelagic phase. Panel b: model

estimated dispersal pattern for *C. rastrospinosus*. Panel c: model estimated dispersal pattern for *C. hamatus*. Panel d: model estimated dispersal pattern for *C. myersi*. The colours of the dots in panels b, c and d represent the number of particles found per model grid cell on the 15th of each month of their dispersal journey and over the 10 years of the model simulation, as shown in the legend. From Schiavon et al. (2021).

4.4.5 Additional research projects

Thanks to the high attraction of RECTO for students and young researchers (for example during the Belgica121 and the ANTXXVII cruises), we could conduct several additional projects, which were not foreseen in the original project application but whose results are highly relevant for science policy and the development of suitable management strategies for the Southern Ocean.

4.4.5.1 Intertidal faunal communities from the Gerlache Strait (Antarctic Peninsula)

The underexplored intertidal ecosystems of Antarctica are facing rapid changes in important environmental factors. Associated with temperature increase, reduction in coastal ice will soon expose new ice-free areas that will be colonized by local or distant biota. To enable detection of future changes in faunal composition, a biodiversity baseline is urgently required. Here, we evaluated intertidal faunal diversity at 13 locations around the Gerlache Strait (western Antarctic Peninsula), using a combination of a quadrat approach, morphological identifications, and genetic characterization. Our data highlight a unique community structure that is typical of disturbed habitats, comprising four generally distributed and abundant species (the flatworm *Obrimoposthia wandeli*, the bivalve *Kidderia subquadrata*, and the gastropods *Laevilitorina umbilicata* and *Laevilitorina caliginosa*) as well as 79 rarer and less widely encountered species. The most abundant species thrive in the intertidal zone, due to their ability to either survive overwinter in situ or to rapidly colonize this zone when conditions allow. In addition, we confirmed the presence of multiple trophic levels at nearly all locations, suggesting that complex inter-specific interactions occur within these communities. Diversity indices contrasted between sampling locations (from 3 to 32 species). Multivariate approaches identified three groups, which relate to environmental parameters such as granulometry, glacial influence, and hydrography. We provided the first genetic and photographic baseline of the Antarctic intertidal fauna (106 sequences, 137 macrophotographs) as well as preliminary insights on the biogeography of several species. Altogether, these results represent a timely catalyst to assess the diversity and resilience of these intertidal communities and have been submitted for publication (Jossart et al. submitted to Biodiversity and Conservation).

4.5.5.2 Anthropogenic impact on macrozoobenthos of the Bransfield Strait: community structure and trace metal concentrations

King George Island is the most directly impacted region by anthropogenic activities in Antarctica, with a permanent village, many research stations and tourist activities. Even though research on macrozoobenthos at the Antarctic Peninsula is increasing, knowledge on its community structure and trace metal concentrations due to human activities is scarce. Therefore, the Peruvian ANTARXII expedition provided a unique opportunity to obtain samples from the Bransfield Strait in different distance from King George Island, to investigate possible trace metal pollution and its impact on macrozoobenthos. Macrozoobenthos and sediment samples were collected in Bransfield Strait during the two legs of the Peruvian ANTARXII expedition with the Peruvian research vessel BAP Carrasco from

December 2019 to February 2020. Spatial distribution of biodiversity and community composition was determined for the macrozoobenthos in the Bransfield Strait at a higher taxonomic level for the whole community (class) and at the species level for the Asterozoa based on photographs. All samples were collected using a Van Veen grab and the findings were related to five environmental variables that were collected at sampling time with a CTD. Significant differences were found between communities at the class level within the Bransfield Strait, which were mostly driven by water depth and the interaction of depth with O_2. The western side of the Bransfield strait was found to have a higher level of biodiversity and species richness and to be dominated mostly by the presence of bivalves. In contrast, the eastern side was found to be poor in overall biodiversity and dominated by only Ophiuroidea or Amphipoda. The stations sampled at the Admiralty Bay were more similar to these poor areas than to species rich western side of the Bransfield Strait (Fig. 18).

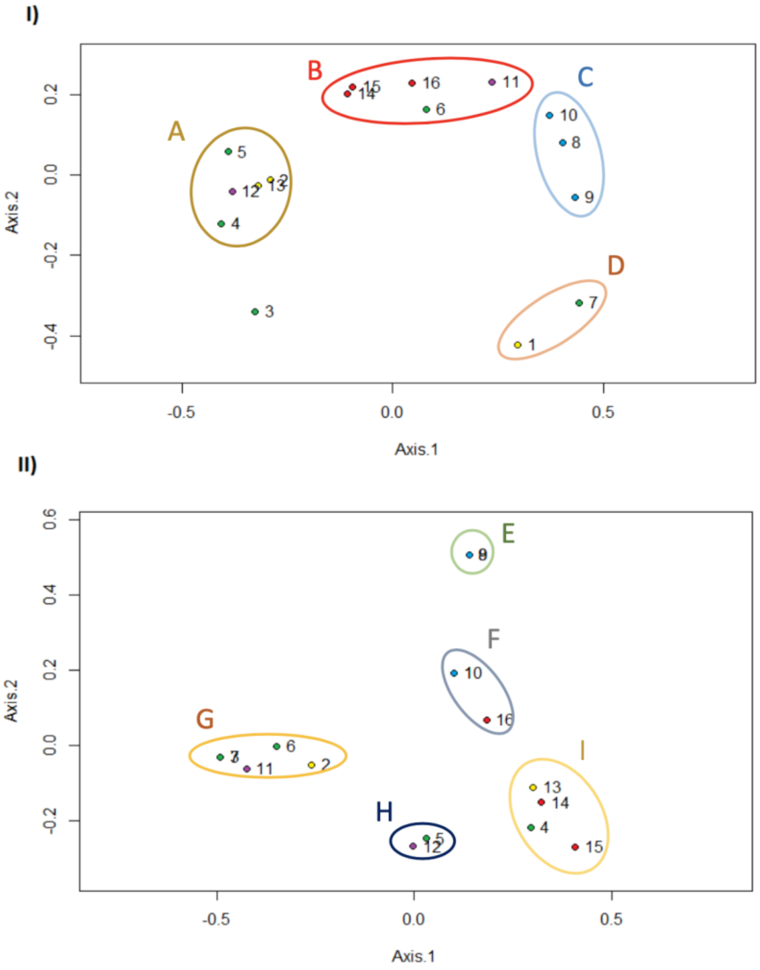


Figure 18: Biplot for the principal coordinate analysis done on the Class abundance data (I), and on the Asterozoa species abundance data (II). Sampling sites are indicated by their station number and colored according to the different geographical locations. Red = Admiralty Bay, purple = Elephant Island, yellow = western Bransfield Strait, green = central Bransfield Strait, blue = eastern Bransfield Strait. Clusters of samplings sites within the PCoA are labelled A to J, and are indicated with coloured ellipses. (Master thesis of Jolien Claes).

Increased human activities in Antarctica as well as long-range pollution pose a potential risk to this fragile ecosystem. The establishment of reference values for trace element concentrations in marine sediments are important for this. This is particularly true in the South Shetland Islands, is the most visited area of the Antarctic continent. 32 sediment samples were collected at 28 stations around King George Island, in the Bransfield Strait and at Hope Bay during the second leg of the Peruvian ANTXXVII campagne. Our results show a clear distinction between the three studied regions but also a high degree of local heterogeneity (Delhaye et al. submitted). The majority of the stations in the Bransfield Strait and around King George Island had moderate to significant enrichment in copper, arsenic and cadmium. All three elements are believed to be from natural origin. Two stations had moderate to heavy arsenic contamination, one presenting a moderate ecological risk. Chromium values at all sampled locations around King George Island were three times higher than those measured between 1994 and 2007. If this is owing to anthropogenic activities remains to be further studied.

5. DISSEMINATION AND VALORISATION

5.1 Organized conferences and workshops

5.1.1 From Taxonomy to Molecular Ecology - workshop in Lima, Peru; 2021

Organized by Quentin Jossart and Marc Kochzius

5.1.2 Biodiversité de l'océan Austral et changement climatique.

Conférences du CEPULB, Brussels, Belgium, Feb 2021, organized by Bruno Danis.

5.1.3 The Belgica121 expedition.

RBINS Nocturne Antarctica, Brussels, Belgium, Feb 2020, organized by Bruno Danis.

5.1.4 Liège Colloquium on Ocean Dynamics "Polar Ocean facing changes"

May 2019, Liège, Belgium; co-organized by Gilles Lepoint.

5.1.5 SCIENTIFIC DIVING IN POLAR ENVIRONMENTS.

Société Belge de Médecine Hyperbare et Subaquatique, 2019, organized by Philippe Dubois.

5.1.6 ON THE PROTEKER (IPEV) PROGRAM AND THE MARINE OBSERVATORY IN KERGUELEN ISLANDS

On board RV Marion Dufresne, for all audiences; 2016 & 2018, organized by Philippe Dubois.

5.1.7 SCAR meeting Leuven

The RECTO consortium played an active part in organizing the SCAR Biology 12th Symposium in 2017, which took place in Leuven, Belgium. 6 RECTO PIs were members of the organisation committee. The main theme for the XIIth SCAR (Scientific Committee on Antarctic Research) biology symposium was "Scale matters". From the small molecular scale, through population and large ecosystem scale, biological processes and diversity span all these levels. Understanding these processes as well past and present patterns of biodiversity are essential for understanding possible threats to Antarctic biology and their impact. With this Symposium, we wanted to focus on understanding biological distribution and trends as well as adaptation and processes both in the marine and terrestrial realm including the human biology. Special attention was paid to multidisciplinary research and how combining insight from different fields could help our understanding of biology in this unique region. An important aspect of this symposium was to focus on the societal impact of Antarctic biological sciences and how this can be communicated, not only to the general public, but also to policy makers. A special issue in *Frontiers* journal was dedicated to the main outcomes of the Symposium. This Research Topic offered the 137 participating authors the opportunity to publish research presented during the SCAR 12th Biology Symposium.

5.1.7 CONFERENCE L'OCEAN ANTARCTIQUE: UN LABORATOIRE POUR L'ETUDE DU CHANGEMENT GLOBAL.

Conférences du CEPULB, Brussels, Belgium, March 2017, organized by Philippe Dubois.

5.2 Press releases B121 & website & Blog & interviews

- B121 expedition: many articles and interviews in the Belgian press, radio and TV. Some examples below:
- KUL Science@Leuven June-August 2019: "Belgica 121: a scientific expedition to the Southern Ocean"
- KUL Campus Krant Junii 2019 "Mariene biologen blikken terug op geslaagde Antarctic-expeditie"
- Le Soir, 8 Feb 2019: https://plus.lesoir.be/205636/article/2019-02-08/au-gre-du-vent-vers-lantarctique-des-chercheurs-belges-en-mission-sur-un-voilier
- BX1, 18 Apr 2019 : https://bx1.be/categories/news/australis-le-voilier-de-chercheurs-qui-a-sillonne-lantarctique/
- HBVL, 9 Jan 2019 : https://www.hbvl.be/cnt/dmf20190107_04084912
- De Standaard, 8 Mar 2019 : https://www.standaard.be/cnt/dmf20190108_04086284
- De Standaard, 9 Mar 2020: https://www.standaard.be/cnt/dmf20200308_04881083
- De Morgen, 20 Feb 2019: https://www.demorgen.be/nieuws/belgen-gaan-vissen-vangen-op-de-zuidpool~b4ad2c54/
- RTBF, 11 Feb 2019: https://www.rtbf.be/info/societe/detail_des-chercheurs-de-l-ulb-partent-a-l-assaut-de-antarctique-en-voilier?id=10136776
- RTBF, 20 Feb 2018: https://www.rtbf.be/info/societe/detail_des-belges-vont-recenser-la-biodiversite-et-le-plastique-dans-l-ocean-austral?id=9845065
- Facebook : https://www.facebook.com/permalink.php?id=548486441978300&story_fbid=1456987957794806

5.3 Other outreach activities to the public

1. 2022: Press release on the RECTO activities at Princess Elisabeth Station (http://www.antarcticstation.org/news_press/news_detail/recto_project_sets_stage_for_future_biological_research)
2. 2021: Permanent information panel about the RECTO project at the temporal exhibition “Antarctica” at the RBINS (Natural History museum, Brussels) (17.10.2019 – 03.01.2021).
3. 2021: youtube movie about RECTO; shot for the Antarctica exhibition but still freely available at youtube and subtitled in several languages (https://www.youtube.com/watch?v=Ty_B6omLu5E)
4. 18/01/2019. Interview for online news portal Stuff New Zealand: Climate change is slowing down Antarctic starfish, Otago scientists find. Joel McManus.
5. 26/01/2017 Interview on Radio New Zealand: Winners or losers? Antarctic starfish and climate change. Allison Ballance.
6. 5/12/2016 Interview by stuff: Antarctic starfish may show climate change will produce winners and losers. Will Harvie
7. 20/10/2016 Interview on the impact of global change in oceans; Newspaper La Libre Belgique, V. Dauchot

5.4 Project meetings, also with follow-up committee

- Final (virtual) project meeting with follow-up committee at zoom: 5.3. & 8.3.21 (42 participants)
- Annual project meeting with follow-up committee 2019 at the RBINS: 21.01.2020 (25 participants)
- Annual project meeting with follow-up committee 2018: 29.11.2018 at Belspo (20 participants)
- Annual project meeting with follow-up committee 2017: 12.07.2017 at the SCAR Biology meeting, Leuven (30 participants)
- Annual scientific project meetings 2017: 17.03.17 at Belspo (15 participants) & 09.11.17 at Belspo (24 participants)
- Annual project meeting with follow-up committee 2016: 25.11.16 at Belspo (10 participants)
- Kick-off meeting: 31.05.16 at Belspo (20 participants)

5.5 Topical project meetings (Formal meetings)

(there were also countless informal meetings among RECTO partners on all topics of the project, which are not specifically listed here)

- Antarctic amphipods: 04.02.16 & 10.07.2020 at RBINS (7 & 5 participants)
- Participation in the Peruvian ANTARXXVII cruise 2019 at RBINS (9 participants)
- Modelling: 15.03.16 (5 participants) & 10.02.17 (5 participants) & 29.11.2018 (3 participants)
- Data management: 21.04.2017 at Belspo (8 participants)
- Active participation in SCAR Biology meeting 2017: 6 RECTO PIs were members of the organisation committee.
- B120 & B121 expeditions: 17.3.17 (15 participants) & 20.4.17 (12 participants)
- Molecular methods: 25.11.16 at Belspo (10 participants) & 10.03.17 at KUL (20 participants)
- Antarctic fish: 16.03.16 at KUL (7 participants)

5.6 Participation of RECTO scientists in conferences and workshops

2022

- **Zoology, 22-23 September 2022, Kortrijk, Belgium**
    - Presentations by Marie Verheye (oral) and Pablo Martinez-Soares (poster – prize for best poster presentation)

2021

- **XXV Congresso AIOL, 30 June-01 July 2021, online**
    - Presentation by Martina Gastaldi (oral)
- **Simposio Genomics Antarctic Biodiversity en el XL Congreso Ciencias del Mar, May 2021, Punta Arenas, Chile, online**
    - Presentation by Zambra López-Farrán (oral)
- **IsoEcol, May 2021** (virtual meeting)
    - Presentation by Anthony Voisin (oral)

2020

- **JCAD, December 2020, Dijon, France**

  - Presentation by Charlene Guillaumot (oral)
- **EVOLMAR (Marine Evolution Italian Congress), November 2020, online**
  - Presentation by Quentin Jossart (oral)
- **1st International Seminar of Risk Management, October 2021, online**
  - Presentation by Louise Delhaye (oral)
- **CNFRA, September 2020, La Rochelle, France**
  - Presentation by Charlene Guillaumot (oral)
- **SCAR Open Science Conference, August 2020, online**
  - Presentation by Zambra López-Farrán (poster), Charlene Guillaumot (oral), M. Arnould-Pétré (oral),
- **Reunión Anual Conjunta Marzo 2020 (LXII Reunión Anual Sociedad de Biología de Chile, XIII SOCEVOL, XXVI SOCECOL, XXIX Reunión Anual Sociedad de Botánica de Chile), March 2020, Valdivia, Chile**
  - Presentation by Zambra López-Farrán (oral)

2019

- **RAS Workshop (Trait data and invasive species), November 2019**
  - Participation by Quentin Jossart
- **IX Congreso Chileno de Investigaciones Antárticas, 3-5 Oct. 2019, Olmue, Chile**
  - Presentation by Zambra López-Farrán (oral)
- **Conference SINAPSIS 2019, October 2019, Gent, Belgium**
  - Presentation by Isa Schön (keynote)
  - Participation of Louraine Salabao
- **Fifth International Marine Connectivity Conference (iMarCo), Sep. 2019, Aveiro, Portugal**
  - Presentation by Valerie Duliere (oral) and Zambra López-Farrán (oral)
- **The Italian Society for Evolutionary Biology (SIBE-ISEB) 8th Congress, Sep 2019, Padova, Italy**
  - Presentation by Luca Schiavon (poster)
- **III International Conference Island Biology 2019, July 2019, Saint-Denis, La Réunion.**
  - Presentation by Zambra López-Farrán (poster)
- **Liège Colloquium on Ocean Dynamics “Polar Ocean facing changes”, May 2019, Liège, Belgium.**
  - Presentations by Isa Schön (oral), Louraine Salabao (poster), Valerie Duliere (poster), Baptist Le Bourg (poster), Zambra López-Farrán (poster)
- **APECS International Online Conference May 2019**
  - Presentations by Louraine Salabao (oral), Tim Plevoets (oral)
- **DEB Symposium, Brest, France, April 2019**
  - Presentation by Charlene Guillaumot (oral)
- **VLIZ Marine Day, March 2019**
  - Presentations by Louraine Salabao (poster), Tim Plevoets (poster)

2018

- **Zoology 2018, Antwerp, Belgium, 13-15 December 2018**

  - Presentations by Marie Verheye (oral), Charlene Guillaumot (oral & poster), Isa Schön (poster), Louraine Salabao (poster), Tim Plevoets (poster)
- **CCAMLR meeting 2018, Hobart, Australia, 22.10-02.11.2018**
  - Participation of Anton Van de Putte
- **RADseq Data Analysis Workshop, Berlin, Germany, July 2018**
  - Participation by Quentin Jossart
- **Centre Interuniversitaire de Biologie Marine (CIBIM) meeting**, **October 2018**
  - Presentation by Quentin Jossaert (oral)
- **11th International Conference on the Applications of Stable Isotope Techniques to Ecological Studie (IsoEcol 2018) at Viña Del Mar (Chile), July 30th-August 3rd 2018**
  - Presentations by Baptiste Le Bourg (oral), Quentin Peignot (poster)
- **SCAR Life Sciences meeting, Davos, Switzerland, 18.6.2018**
  - Participation of Anton Van de Putte
- **POLAR 18: SCAR/IASC Open Science Conference, Davos, Switzerland, 18-26 June 2018**
  - Presentations by Charlene Guillaumot (oral), Franz Heindler (oral & posters)
  - Participation of Anton Van de Putte & Bruno Danis
- **RAATD meeting, Davos, Switzerland, 16.6.2018**
  - Participation of Anton Van de Putte
- **SCADM meeting, Davos, Switzerland, 15-17.6.2018**
  - Organization & participation of Anton Van de Putte
- **16th International Echinoderm Conference, Nagoya, Japan, 31/05/2018**
  - Presentation by Baptiste Le Bourg (oral) & Philippe Dubois (oral)
- **Marine Evolution, Strömstad, Sweden, 15-17 May 2018**
  - Presentation by Henrik Christiansen (poster)
- **OBIS Tracking workshop, Hobart, Australia, 23-26/4/2018**
  - Participation of Anton Van de Putte
- **MEASO, Hobart, Australia, 9-13 April 2018**
  - Presentation by Charlene Guillaumot (oral)
  - Participation of Anton Van de Putte
- **CCAMLR EU workshop, Brussels, Belgium, 12 April 2018**
  - Participation of Bruno Danis
- **MEASO congress, Hobart, Australia, 9-12 April 2018**
  - Presentations by Anton Van de Putte (oral), Charlène Guillaumot (poster & oral), Thomas Saucède (poster), Marc Elaume (poster)
- **VLIZ Marine Science Day March 2018**
  - Presentation by Nina Dehnhard (oral)

2017

- **International Workshop on Sharing, Citation and Publication of Scientific Data across Disciplines, 5–7 December 2017, Tokyo, Japan**
  - Presentations of Anton Van de Putte (oral & 2 posters)
- **Zoology 2017, November 2017, Wageningen, The Netherlands**
  - Presentations by Bruno Fréderich (poster), Baptiste Le Bourg (poster), Quentin Peignot (poster)

  - Participation of Gilles Lepoint
- **Kerguelen Symposium, November 2017**
  - Presentation by Charlène Guillaumot (oral)
- **Antarctic Ecosystem Research following Ice Shelf Collapse and Iceberg Calving Events. 18-19 November 2017, Florida State University Coastal and Marine Laboratory, Florida, USA**
  - Participation of Anton Van de Putte
- **Congreso de Ciencias Antarcticas (Punta Arenas), 30 September – 8 October 2017**
  - Participation of Bruno Danis, Camillle Morea, Thomas Saucède
- **12th SETAC Latin America Biennal Meeting", Santos, Brazil, September 2017**
  - Presentation by J.D. Padilha (poster)
- **Waterbird Society Annual Meeting 2017, Reykjavik, Iceland, 11 August 2017**
  - Presentation by Nina Dehnhard (oral)
- **SCAR Biology (Leuven, Belgium), 10-14 July 2017**
  - Presentations by Antonio Agüera (oral), Philippe Dubois (oral & poster), Nina Dehnhard (oral), Sarah Di Giglio (poster), Cedric d'Udekem d'Acoz (poster), Valèrie Dulière (poster), Cyril Gallut (oral), Charlène Guillaumot (oral), Franz M. Heindler (poster), Baptiste Lebourg (oral), Franscesca Pasotti (oral), Henri Robert (poster), Isa Schön (poster)
  - Participation of Bruno Danis (scientific organization committee), Anton Van de Putte (Chair Local Organization committee), Filip Volckaert (Local organization committee), Chantal De Ridder (scientific organization committee), Bruno Frederich, Gilles Lepoint
- **JERICO-next Summer school** (la Haye, Netherlands), 19-23 June 2017
  - Participation of Charlène Guillaumot
- **Semin'R workshop** (Paris, France), 16 June 2017.
  - Presentation by Charlène Guillaumot (oral).
- **DEB Symposium** (Tromso, Norway), 31 May - 2 June 2017.
  - Presentation by Charlène Guillaumot (oral).
- **Developing the West Antarctic Peninsula International Network within the Southern Ocean Observing System workshop**, 15-16/05/2017, Cambridge, United Kingdom
  - Presentations by Michel L. N. (poster), Charlène Guillaumot (poster), participation of Antonio Agüera
- **13èmes Journées Scientifiques du Comité National Français de Recherches Arctiques et Antarctiques (CNFRA), 11-12/05/2017, Paris, France**
  - Presentations by Thomas Saucède (oral), Agnès Dettaï (oral), Charlène Guillaumot (oral)
- **Benelux Association of Stable Isotope Scientists (BASIS) symposium** 2017, 03-04/05/2017, Utrecht, The Netherlands.
  - Presentation by Loïc Michel (oral)
- **Arctic Science Summit Week & EU-PolarNet General Assembly**, 31/03-07/04/2017,Prague, Czech Republic
  - Participation of Anton Van de Putte
- **Bioinformatics Workshop**: on 31/03/2017 organised by Genomics Core KUL at KUL
  - Participation of Franz M. Heindler, Filip Volckaert, Francesca Pasotti, Henri Robert.
- **RAATD workshop**, Aix-en-Provence, France, 19-24 March 2017

  - Participation of Bruno Danis.
- **VLIZ Marine Science Day ,** 03/03/2017, Brugges, Belgium
  - Presentations by Franz M. Heindler (poster), Loïc Michel (oral), Quentin Peignot (poster)
- **SG OBIS VI, 1-3 February 2017, Okinawa, Japan; steering committee meeting**
  - Participation of Anton Van de Putte
- **International Long Term Ecological Research Network and Zones Ateliers & Critical Zone Observatory Networks Joint Conference, 2017, Nantes, France**
  - Presentation by Philippe Dubois (oral)

2016

- **Zoology 2016**, Antwerp, Belgium, 16.-17.12.16
  - Presentations by F.M. Heindler (poster), B. Le Bourg (oral)
  - Participation of Isa Schön, Gilles Lepoint, Bruno Frederich.
- **Taxonomy Workshop,** Concarneau, France, 25-29 Oct 2016
  - Participation of Bruno Danis.
- **Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR)** meeting, 18.-28.10.2016, Hobart, Australia
  - Participation of Anton Van de Putte.
- **“Register of Antarctic Species”,** Ostend; Belgium, 20.-22.9.2016
  - Organization by Anton Van de Putte; participation of Bruno Danis.
- **EU Polar Net, Town Hall event,** Brussels, Belgium, 27.09.2016
  - Participation of Isa Schön & Anton Van de Putte
- **Joint European Stable Isotopes User group Meeting (JESIUM) 2016**, 05/09/2016, Ghent, Belgium.
  - Presentations by Baptist Le Bourg (poster), Loic Michel (poster).
- **SCAR Open Science Meeting** (Kuala-Lumpur, Malaysia), 20-30 August 2016.
  - Participation of Anton Van de Putte, Antonio Agüera, Camille Moreau.
- **Ciencia 2016, 4-6.7.2016, Lisboa, Portugal**
  - Presentation by Anton Van de Putte (oral).
- **ETN Workshop**, Bremerhaven, Germany, 19-20 May 2016
  - Participation of Bruno Danis.
- **BNCGG-BNCAR symposium, “Unlocking a continent: scientific research at the Belgian Princess Elisabeth Station, Antarctica 2008-2016**”, 29.04.16, Brussels, Belgium
  - Presentations by Loic Michel (poster), Isa Schön (poster)
  - Participation of Bruno Danis, Gilles Lepoint, Marc Kochzius, Anton Van de Putte, Bruno Frederich & Antonia Agüera.
- **10th International Conference on the Applications of Stable Isotope Techniques to Ecological Studies** (IsoEcol 2016), 08/04/2016, Tokyo, Japan.
  - Presentation of Loic Michel (oral).
- **VLIZ Marine Science Day 2016**, 12/02/2016, Bruges, Belgium
  - Presentations by FranzM. Heindler (poster), Baptist Le Bourg (poster), Loic Michel (poster).

5.7 RECTO Students and early career researchers

Post docs

1. Valerie Duliere (RBINS)
2. Antonio Agüera (ULB)
3. Quentin Jossart (VUB & ULB)
4. Zambra López-Farrán (RBINS) – external funding
5. Camille Moreau (ULB)
6. Bruno Frédérich (ULiège) – external funding
7. Loic Michel (ULiège) – external funding
8. Marie Verheye (ULiège & RBINS) – external funding
9. Francesca Pasotti (UGent)

PhD students:

10. Charlène Guillaumot (ULB) – external funding
11. Coline Marciau (PhD ULB) – external funding
12. Lea Katz (PhD student ULB)
13. Louraine Salabao (ULiège, UHasselt) – external funding
14. Baptiste Le Bourg (ULiège)
15. Franz Maximilian Heindler (KUL)
16. Henrik Christiansen (KUL)

MSc students:

17. Severino Suzie (ULIège)
18. Lore Van Craenenbroek (UGent & RBINS)
19. Eleonora Cariolato (UGent & RBINS)
20. Jolien Claes (VUB)
21. Louise Delhaye (VUB)
22. Quinton Engelbrecht (VUB)
23. Tim Plevoets (VUB & RBINS)
24. Quentin Peignot (Université de Reims & ULiège)
25. Nicolas Gamb (Aix-Marseilles Université & ULiège)
26. Anouk Charpentier (Aix-Marseilles Université & ULiège)
27. Déborah Faria Nardi (ULiège).
28. Alix Kristiansen (Sorbonne Université, ULiège, Ifremer Brittany)
29. Anthony Voisin (ULiège, Ifremer Brittany)
30. Baricalla Jonathan (ULiège)
31. Manon Bayat (ULB)
32. Jeanne Dreidemy (ULB)
33. Margot Mathieu (ULB)
34. Maureen Kassel (ULB)
35. Floriane Barot (ULB)
36. Jeanne Dreidemy (ULB)
37. Laura Demoustier (ULB
38. Arnould-Pétré (ULB-UBFC)
39. Luka Vantomme (ULB-IMBRSEA/UGENT)

40. Galadriel Guillen (ULB-CEBC/CNRS)
41. Laura Meudec (ULB-MNHN)
42. Marie Lefebvre (ULB-ULILLE)

BSc students:

43. Phaedra Ools (UHasselt/RBINS)
44. Julien Duysen (ULiège)
45. Yelle Vandenboer (UHasselt/RBINS, ULiège)
46. Julien Duysen (Haute Ecole Liège Meuse Ourthe, ULiège)

Interns:

47. Louraine Salabao (RBINS)
48. Warren Caneos (RBINS)
49. Marius Buydens (RBINS)
50. Rey Harvey Suello (RBINS)
51. Sauna Rumba (RBINS)
52. Nadia Shymboliova (RBINS)
53. Debora Mussa Benjamen (RBINS)
54. Rose Antoneth Loquere (RBINS)
55. Kugonza Priscilla (RBINS)
56. Galadriel Guillen (ULB)
57. Laura Meudec (ULB)
58. Alexia Dimopoulos (ULB)
59. Dorine Schlechts (ULB)
60. Pablo Martinez (ULB-MNHN)
61. Samantha Rush (ULB)
62. Galadriel Guillen (ULB)
63. Nergiz Ducan (UGent, RBINS)

6. PUBLICATIONS

6.1 A1 publications

A1 publications in press

1. **Delhaye L.,** Elskens M., Ricaurte-Villota C., Cerpa L. & **Kochzius M.** (submitted). Baseline concentrations, spatial distribution and origins of trace elements in the surface sediments of the Bransfield Strait, Antarctica. *Marine Pollution Bulletin*.
2. **Guillaumot C., López-Farrán Z.** (co-firstauthorship), Vargas-Chacoff L., Paschke K., **Dulière V., Danis B.,** Poulin E., **Saucède T.** & Gerard K. (in press). Current and predicted invasive capacity of *Halicarcinus planatus* (Fabricius, 1775) in the Antarctic Peninsula. *Global Change Biology*.
3. Fabri-Ruiz S., **Guillaumot C., Agüera A., Danis B. & Saucède T.** (in press). Using correlative and mechanistic niche models to assess the sensitivity of the Antarctic echinoid *Sterechinus neumayeri* (Meissner, 1900) to climate change. *Polar Biology*.
4. **Jossart Q., Bauman D., Moreau C., Saucède T., Christiansen H.,** Brasier M.J., Convey P., Downey R., Figuerola B., **Martin P.,** Norenburg J., Rosenfeld S., **Verheye M. & Danis B.** (submitted). The dominant, the rare and the unexpected: a pioneer in situ, morphological and genetic investigation of the intertidal communities from the Gerlache Strait (Antarctica). *Biodiversity and Conservation*.
5. Parker E., Zapfe K.L., Yadav J., Frédérich B., Jones C.D., Economo E.P., Federman S., Near T.J. & Dornburg A. 2022. Periodic environmental disturbance drives repeated ecomorphological diversification in an adaptive radiation of Antarctic fishes. *American Naturalist*. (in press)

A1 publications 2022

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58. **Le Bourg, B.,** Kuklinski P., Balazy P., **Lepoint G.,& Michel L.N.** (2021). Interactive effects of body size and environmental gradient on the trophic ecology of sea stars in an Antarctic fjord. Submitted to *Marine Ecology Progress Series*.

A1 publications in preparation

1. **Christiansen, H., Dulière, V., Heindler, F.M**., Geslain, E., Bista, I., **Van de Putte, A.P., Young, E., Schön, I. & Volckaert, F.A.M.** Genetic structure and connectivity of four high-Antarctic fishes in relation to ocean currents.
2. **Christiansen, H., Heindler, F.M., Dettai**, A., Collins, M.A., Couloux, A., Duhamel, G., Hautecoeur, M., Steinke, D., **Volckaert, F.A.M., Van de Putte, A.P**. Diversity of mesopelagic fishes in the Southern Ocean - a phylogeographic perspective.
3. **Christiansen, H., Heindler, F.M., Van de Putte, A.P. & Volckaert, F.A.M.** Genomic differentiation and local adaptation associated with contrasting climate change in an Antarctic fish**.**
4. **Christiansen, H., Van de Putte, A. P., Guillaumot, C.,** Barrera-Oro, E**., Volckaert, F.A.M. & Young, E.** Large scale connectivity in the Southern Ocean revealed through population genomics of historically overexploited fish.
5. **Christiansen, H., Heindler, F.M**., Geslain, E., Bista, I., **Frédérich, B., Dettai, A., Moreau, C.,** Hellemans, B., **Van de Putte, A.P., Schön, I. & Volckaert, F.A.M.** Genomic divergence in ecologically diverse Antarctic fish**.**
6. **Cordone E.**, **Vanreusel A., Pasotti F., Schön I**. Population genomics of the bivalve Antarctic species *Laternula elliptica*: a mtDNA approach to evolutionary history paths.
7. **Heindler, F.M**.*, **Christiansen, H**.*, Maes, S.M.T., **Frederich, B., Michel, L.N., Dettai, A**., Desvignes, T., Maes, G.E., **Van de Putte, A.P., & Volckaert, F.A.M**. Combined microbiome and stomach content DNA metabarcoding demonstrates novel food web links and microbiome-host interactions along an evolutionary bentho-pelagic gradient in fishes of the Southern Ocean. *equal contribution.
8. **Jossart Q.,** Moreau C., **Dettaï A., Danis B. & Kochzius M.** Sea star mitogenomes: characterization and utility for phylogenetics.
9. **Jossart Q, Moreau C, Kochzius M, Danis B,** Hellemans B**, Christiansen H.** Depth-differentiation in the sea star *Bathybiaster loripes* revealed from the joint-use of mtDNA and reduced representation sequencing data.
10. **López-Farrán Z.,** José Frugone M., Gerard K., Vargas-Chacoff L., **Guillaumot C., Dulière V.,** Ledoux J.-B., Waters J. & Poulin E. Evaluation of the dispersion scale across of Southern Ocean of *Halicarcinus planatus* and its reach to the Antarctic Peninsula.
11. **Pasotti F., Vanreusel A., Schön I**. Complete mitochondrial genome of the non-model Antarctic bivalve *Aequiyoldia eightsii* (Bivalvia; Nuculida).
12. **Robert H**., Vigin L., **Van de Putte A., Schön I**. Population biology of snow petrels in the Sor Rondane Mountains, Queen Maud Land, Antarctica.
13. **Salabao L., Lepoint G., Frédérich B., Kochzius M. & Schön I**. Thermal adaptation of polar amphipods derived from mitogenomic data.
14. **Van Craenenbroek L., Dunca, N,. Pasotti F., Vanreusel A., Schön I**. Population history of the bivalve *Aequiyoldia eightsii* from RAD seq and mitochondrial data.
15. **Verheye M.L.**, Maes G., **Schön I. & Van de Putte A**. Genetic diversity and connectivity of the *Eusirus perdentatus* species complex (Amphipoda, Crustacea) on the Antarctic continental shelf.

16. **Verheye M.L. & d'Udekem d'Acoz C**. Contribution to the systematics of crested *Eusirus* in the Southern Ocean, with the description of a new species (Crustacea, Amphipodan Eusiridae).

6.2 Other publications

1. **Danis, B, Christiansen, H. Guillaumot, C., Heindler, F.,** Houston, R., **Jossart, Q.,** Lucas, K., **Moreau, C., Pasotti, F., Robert, H.,** Wallis, B., **Saucède, T.** 2019. Report of the Belgica 121 expedition to the West Antarctic Peninsula. 96 pp.
2. Brandt, A., Di Franco, D., Griffiths, H., Jerosch, K., **Verheye, M., Volckaert, F., Christiansen, H., Danis, B., Lepoint, G., Linse, K., Schön, I., Van de Putte, A.** 2019. Integrated macro- and megabenthic characterization of the Weddell Sea. In: The Expedition PS118 of the Research Vessel POLARSTERN to the Weddell Sea in 2019 (ed Dorschel B). Reports on Polar and Marine Research, 735, 149p, doi:10.2312/BzPM_0735_2019.
3. Motreuil S., **Dubois P., Michel L.,** Gonthier-Maurin M., Bertrand G., Marschal C., **Saucède, T.** 2016. PROTEKER, rapport de campagne d'été 2018/2019. Impact du changement global sur le benthos et les habitats marins côtiers des Iles Kerguelen. http://www.proteker.net/IMG/pdf/proteker_2016-2017_rapport_xs.pdf

6.3 Abstracts

Abstracts 2022

1. **Verheye Marie L., Herrel A., Lepoint G., Martinez-Soares P., Schön I., Frédérich B.** 2022. Antarctica as an evolutionary incubator? Phylogenetic comparative study of the amphipod family Iphimediidae on the Antarctic shelf. Zoology 2022, Campus KULAK, Kortrijk, 22-23 September 2022.
2. **Martinez-Soares P.**, Herrel A.**, Frédérich B., Lepoint G.**, Castrec C.**, Michel L., Verheye M.L.** 2022. Diversity in mouthpart morphology and trophic niche in Antarctic Iphimediidae (Amphipoda). Zoology 2022, Campus KULAK, Kortrijk, 22-23 September 2022 – best poster award

Abstracts 2021

3. **Verheye, M.,** Herrel, A., **Frederich, B**., Castrec, C. & **Michel, L., & Lepoint, G.** 2021. How mandible morphology relates to trophic ecology in Antarctic amphipods: the case of Iphimediidae revealed by 3D-Geometric Morphometrics and Stable Isotopes. Poster session presented at Society for Integrative and Comparative Biology 2021 Virtual Annual Meeting.
4. **Voisin A., Lepoint G., Danis B., Guillaumot C**., Kristiansen A., **Pasotti F., Saucède T. & Michel L.N.** 2021. Food web structure in a rapidly changing coastal environment: the West Antarctic Peninsula. IsoEcol 2021 – virtual meeting.

Abstracts 2020

5. Arnould-Pétré M, **Guillaumot C, Danis B,** Féral J-P, **Saucède T.** 2020. Individual-based model of population dynamics in Abatus cordatus, a sea urchin endemic to the Kerguelen Plateau, under changing environmental conditions. SCAR Symposium, Hobart, Tasmania, August 2020.

6. **Guillaumot C,** Kooijman S, **Danis B, Saucède T.** 2020. Application of Dynamic Energy Budget (DEB) models to Antarctic case studies. SCAR Symposium, Hobart, Tasmania, August 2020.
7. **Guillaumot C,** Kooijman S, **Saucède T, Danis B.** 2020. Application des modèles de budget énergétique (Dynamic Energy Budget, DEB) à des cas d'étude polaires. CNFRA, La Rochelle, France, September 2020.
8. **Guillaumot C, Saucède T, Danis B.** 2020. Les modèles de niche écologique, outils pour évaluer la sensibilité des espèces marines antarctiques face aux changements environnementaux: potentiel, limites et méthodes. JCAD, Dijon, France, December 2020.
9. López-Farrán Z, Frugone MJ, Vargas-Chacoff L, **Guillaumot C,** Gerard K, Poulin E, **Dulière V.** 2020. Assessment of the capacity of *Halicarcinus planatus* to arrive and settle as a potential invasor of Antarctic shallow ecosystems. SCAR Symposium, Hobart, Tasmania, August 2020.

Abstracts 2019

10. **Dulière V, Christiansen H, Heindler FM,** Papetti C, **Pasotti F,** Schiavon L & **Schön I.** 2019. Past and future dispersal of Antarctica species: a Lagrangian modeling tool. 51rst Ocean Colloquium, Liège: Polar Oceans facing changes.
11. **Dulière V., Heindler M.F., Christiansen H., Lacroix G., Volckaert F.A.M. & Schön I.** 2019. Combined approaches in support to study refugia and ecosystem tolerance in the Southern Ocean. Fifth International Marine Connectivity Conference (iMarCo), 23-25 Sep. 2019, Aveiro, Portugal.
12. **Guillaumot C,** Artois J, **Saucède T & Danis B.** 2019. Broad-scale species distribution models applied to data-poor areas. ISEM, Salzburg, Austria, October 2019.
13. **Guillaumot C, Saucède T & Danis B.** 2019. Assessing the response of a simple bentho-pelagic network to environmental changes: case study from the Southern Ocean. DEB Symposium, Brest, France 1-12/04/2019.
14. Guillaumot C, Saucède T & Danis B. 2019. Ecological niche modelling as a tool to assess the sensitivity of Antarctic marine species to environmental changes: potential, limitations and methods. Forum des Jeunes Chercheurs, Dijon, France, June 2019.
15. **Guillaumot C, Saucède T & Danis B. 2019.** Inferring the response of Southern Ocean benthic species to environmental changes using Dynamic Energy Budget models. DEB Symposium, Brest, France, April 2019
16. **Le Bourg, B.,** Blanchard, A., **Danis, B., Jossart, Q., Lepoint, G., Moreau, C., & Michel, L.** 2019. Environmental drivers of sea stars feeding ecology in the Southern Ocean. 51rst Ocean Colloquium, Liège: Polar Oceans facing changes. http://hdl.handle.net/2268/235407
17. **López-Farrán Z,** Frugone MJ, Vargas-Chacoff L, **Guillaumot C,** Gerard K, Poulin E & **Dulière V** 2019. *Halicarcinus planatus*, la primera especie exótica encontrada en la Península Antártica: Evaluación de su potencial invasor. Reunión Anual Conjunta 2019, Valdivia, Chile, November 2019
18. **López-Farrán Z, Guillaumot C, Dulière V,** Paschke K, Gerard K, Vargas-Chacoff L & Poulin E. 2019. *Halicarcinus planatus*, el cangrejo subantártico con potencial para establecerse en Antártica, evaluación del escenario actual y futuro. IX Congreso Chileno de Investigaciones Antárticas, Olmue, Chile, October 2019.
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6.4 Data sets in open repository or data papers

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ANNEXES

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