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