Summary in English

Although both polar oceans share traits like high-latitude location and seasonal ice cover, they differ significantly in oceanographic conditions that shape marine biodiversity and distribution patterns. The Arctic is increasingly influenced by warm Atlantic Water presence, leading to borealization and the arrival of temperate species, while the Antarctic remains more isolated due to the Antarctic Circumpolar Current. However, climate-driven shifts such as warming waters, changing currents, and poleward-moving fronts may allow subpolar species to expand southward, potentially displacing cold-adapted polar taxa. These large-scale environmental shifts have renewed interest in biogeographic patterns such as bipolarity, where similar or closely related taxa are found in both polar regions but are absent from intervening temperate zones. Understanding how such disjunct distributions arise and are maintained is critical for assessing species' responses to ongoing climate change, especially as warming oceans may disrupt the isolation that once supported these patterns. Zooplankton communities, which form the foundation of marine food webs, are particularly sensitive to such changes. To fully understand the ecological scope and consequences of these shifts, it is essential to investigate not only dominant zooplankton taxa but also understudied groups. One such group is Ostracoda, for which foundational data on biogeographical distribution, reproductive systems, and genetic diversity are still emerging. This makes them a timely and revealing model for testing the persistence and mechanisms of bipolarity in the face of environmental change.

Ostracods are tiny calcareous organisms that have the ability to biomineralize, so their calcitic shells are key for paleoenvironmental reconstruction. As a result, they are the most abundant arthropod group in the fossil record, with reliable dating back to the Ordovician period over 400 million years ago. However, this also means that like other calcareous taxa, modern living populations are sensitive to changing water parameters. While much is known about freshwater ostracods, particularly those from the benthos, unfortunately, the same is not true for marine pelagic species. Pelagic ostracods are a cosmopolitan taxon present in all oceans with a ubiquitous range in the water column, from the surface to the deep-sea. They are taxonomically separated into Myodocopida, comprising benthic and epibenthic species, and Halocyprida which represent exclusively pelagic species. Benthic species can be readily collected and studied but there is little knowledge about the biology, evolutionary history, and biogeography of pelagic marine ostracods. Halocyrpids are a significant component of mesopelagic ecosystems across global oceans, but

compared to other planktonic taxa such as copepods, these pelagic species remain largely absent from ecological and molecular syntheses. With seven distinct life stages and a lack of taxonomic experts for halocyprids, this knowledge gap presents both a challenge and an opportunity. The scarcity of information ensures that new contributions offer valuable insights into the evolutionary roles of these microcrustaceans.

The overarching hypothesis was to test whether polar pelagic ostracods have underlying biological and genetic divergences shaped by unique environmental pressures at each pole; if so, these divergences challenge the assumption of ecological and evolutionary symmetry across polar regions and suggest that oceanographic changes may differentially disrupt reproductive stability and genomic integrity in these cold-adapted taxa. This PhD thesis addresses this hypothesis by expanding the current understanding of these polar halocyprids through four integrated studies. The first is a systematic review that provides a complete overview of the latitudinal disjunct distributions of marine taxa, with an emphasis on polar representation. The second and third studies investigate reproductive dynamics in polar halocyprids, revealing unusual patterns of sex ratios and the presence of intersexuality in Arctic species, potentially linked to environmental or developmental stressors. Finally, the fourth study employs mitochondrial genome data to explore structural differences and similarities among key polar halocyprid species, offering a rare genetic perspective in a group with limited molecular resources. Together, these studies advance the foundational understanding of halocyprid ostracods at both poles and highlight their importance in marine biodiversity and evolutionary research.

Purpose of Research

The goal of this thesis was to investigate the bipolarity concept, with pelagic ostracods as model organisms. This PhD thesis is comprised of four studies, whose research objectives are:

1) To review and synthesize the current status of disjunct distribution of marine taxa research by:
    - Exploring the spatiotemporal trends, extent of molecular evidence, and taxonomic representation
    - Confirming potential bipolarity in publicly available databases using global distribution data
2) To investigate the life history trait of sex ratio in polar ostracods by:

- Using historic and contemporary sex data from both Arctic and Antarctic Waters
- Exploring potential ecological or geographic influences on variation

3) To report the first observations of reproductive abnormalities in Ostracoda by:
    - Assessing the extent of Arctic ostracods with atypical sexual morphology
    - Verifying presence of intersexuality in Antarctic specimens in historic collections
4) To determine if polar halocyprid ostracods differ genetically from temperate species by:
    - Characterizing the mitochondrial genome of genera considered bipolar (i.e., *Boroecia* and *Obtusoecia*) and a cosmopolitan genus (i.e., *Discoconchoecia*)
    - Comparing structural modifications within and between ostracod families

Synopsis of Research Works

The first article [1] presents a systematic review of the current state of knowledge on the complex disjunct latitudinal distributions of marine organisms, including both bipolarity (when identical or closely related taxa occur only in the polar waters of both hemispheres) and antitropicality (referring to species that only occur within the temperate zones of both hemispheres, avoiding the tropics). Remarkably, many records labeled as "bipolar" actually describe antitropical patterns, calling into question the accuracy and consistency of terminology use. Moreover, several widely cited “bipolar” examples lack clear spatial evidence or rigorous criteria, pointing to an inflation of these terms in the literature. By compiling and analyzing 665 records from 221 articles, this publication provides a critical synthesis of bipolar and antitropical research on marine species across taxa and time. The analysis identifies distinct biases in taxonomic and geographic representation. Antitropical records were disproportionately dominated by vertebrates largely due to better sampling, higher visibility, and commercial interest, whereas bipolar records include more invertebrate taxa, often reflecting stronger historical ties to polar-focused research. While molecular tools are necessary to accurately identify and verify disjunct distributions, only a quarter of records used genetic evidence in conjunction with morphological data. As the first study to compile all previous literature on latitudinally disjunct distributions, this study fills a need by the biogeographic community at a critical point in time, especially as “bipolarity” grows as a buzzword in the context of climate-driven shifts in marine biodiversity patterns. Within the context of this

PhD, it also introduces the topic of bipolarity, what research has already been done, and cautions terminology usage in this thesis's next publications.

Building on the initial systematic review on latitudinally disjunct distributions [1], the second article [2] transitions from broad distributional patterns to species-level population dynamics at both poles. The second article used Arctic and Antarctic ostracod populations to explore the sex ratio of polar halocyprids and to investigate the factors that influence this ratio including but not limited to depth, season, and species. A uniquely robust dataset was compiled of 507 zooplankton samples over 7 polar expeditions, resulting in thorough analyses that showed a global stability of ostracod sex ratio at first glance. However, when separating between life stages, the pre-adult population at the last stage of development had a higher female proportion than the adults in all species across all factors. If ostracod sex determination is under strong environmental control, this could affect species abundances and subsequent population dynamics. Sex ratios are still rarely mentioned in polar zooplankton reports; however, these data may exist and as shown in this article, can be successfully used as another important feature to describe zooplankton community structure in relation to spatiotemporal aspects. Sexing is often done in parallel with taxonomic identification and these data should be taken into account since deviations of sex ratio in changing oceanographic conditions could potentially have population-wide impacts. While interpreting results, many knowledge gaps arose regarding polar pelagic ostracod species (e.g., reproductive behavior) that should be promptly addressed to determine ecological connections with more confidence.

During routine morphological analyses of the Arctic time series for the sex ratio study [2], many ostracod individuals were discovered to exhibit atypical sexual characteristics that did not align with clearly male or female reproductive structures. These findings prompted a separate investigation, resulting in a dedicated third article on intersex individuals in Arctic ostracod populations [3]. The occurrence of intersex traits, only present in the pre-adult developmental stage and not in fully developed adults, raised important questions about potential environmental or developmental stressors influencing sexual differentiation. By micro-dissecting over 4,000 pre-adult and adult individuals, the 15.6% of intersex individuals present cannot be attributed to chance. These samples were taken annually in the Fram Strait where there is strong mixing of Arctic and Atlantic waters, so this work communicates a decadal (2010-2019), baseline observation of ostracods for future reference. As this is the first documented report of

intersexuality in Ostracoda, it was necessary to verify whether halocyprids from the other pole also displayed similar abnormalities. Therefore, historic Antarctic specimens from the 1930s and 1970s of the same genera were personally analyzed at the Museum of Natural History, London, and there were no cases of intersexuality found. This article sends a cautionary message to other researchers to look out for morphological changes of their target species. Even slight environmentally-induced morphological changes in cryptic species could potentially cause difficulty, so integration of genetics is key to confirm taxonomic identification of modern plankton samples.

In light of these morphological abnormalities, the overall lack of genetic data in polar pelagic ostracods became increasingly apparent, motivating the design of the fourth and final study [4]. In the fourth manuscript, the first complete mitochondrial genomes for five dominant polar halocyprid species, among which the *Boroecia* and *Obtusoecia* genera are still presented to be bipolar. Genomic data for polar-adapted taxa are essential for understanding the evolutionary strategies that enable life in extreme environments and for potentially predicting how these species may respond to rapid climate change. While all five species exhibited the typical metazoan complement of 13 protein-coding genes, two rRNA genes, and 22 tRNAs, several unique features were observed. These include rearrangements in gene order, a consistent split in the *ND3* gene, and structural anomalies in tRNAs that are specific to the Halocyprididae family. This may suggest lineage-specific divergence that reflect deeper evolutionary trajectories or adaptations linked to mitochondrial translation efficiency in cold environments. The relatively shorter mitogenome lengths observed in *Boroecia* species from both poles and the absence of the *ATP8* gene in their initial annotations further underscore the need for cautious interpretation of automatic genome annotations, especially in underrepresented taxa like ostracods. More broadly, the findings establish a foundation for future comparative studies on mitogenomic evolution across latitudes, give insights into mitochondrial genome plasticity in extreme environments, and provide essential reference specimens for improving species identification in metabarcoding applications. By contributing to the growing understanding of how cold-adapted taxa are genomically structured, this article sets the foundation to further explore ostracod genomics and help predict how biodiversity in polar ecosystems may respond to accelerating environmental change.

Collectively, the studies presented in this thesis offer a multifaceted view into the ecology, biogeography, and genomics of polar pelagic ostracods, a group often overlooked in broader discussions of zooplankton diversity and resilience. Each chapter builds on the next, from

conceptual synthesis to population-level observations and from anatomical discovery to molecular insight, establishing an integrated foundation for future studies on the evolution and diversity of these tiny calcareous crustaceans. In doing so, this thesis not only deepens the taxonomic and ecological understanding of halocyprid ostracods, but also underscores the value of holistic, cross-disciplinary approaches to marine biodiversity research. Despite some limitations in the studies, they demonstrate how detailed investigations into seemingly obscure taxa can provide vital clues about the mechanisms underlying biogeographic patterns and biological responses to climate stressors. While the phenomenon of bipolarity is rare, in the case of halocyprid ostracods, with their widespread but patchy distributions, complex reproductive systems, and genomic uniqueness conserved within the halocyprid family, they can be a good model for understanding disjunct distributions in a warming world and help identify early warning signals of ecosystem restructuring. Overall, this thesis helps set the groundwork for more inclusive and comprehensive models of biodiversity change in polar oceans and highlights the importance of continuing to look beyond the usual indicator species when assessing the future of marine life under climate change.

Achievements

- Advanced understanding of bipolarity [1] through pelagic ostracods' sexual differentiation [2,3] and genetic structuring [4]
- Combined morphological and developmental data from halocyprid ostracods [2][3] to investigate reproductive patterns, uncovering consistent pre-adult sex biases [2] and subsequent sexual abnormalities [3]
- Produced the first record of intersexuality [3] and five new mitogenomes [4] for halocyprids, enabling future evolutionary, taxonomic, and metabarcoding research
- Incorporated historic and contemporary material to broaden biogeographic and temporal coverage [1,2,3,4]