Macrozooplankton from Crozet to Kerguelen and Subtropical Southern Indian Ocean

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Abstract:

This paper investigates the spatial distribution of macrozooplankton across various hydrological regions within the Southern Indian Ocean and the Southern Ocean, encompassing the Crozet and Kerguelen archipelagos in the Southern Ocean, and the islands of Saint-Paul and New Amsterdam in the Southern Indian Ocean. Data used in this study were gathered during the REPCCOAI surveys conducted during the summers from 2017 to 2019 aboard the R/V *Marion Dufresne II*. Macrozooplankton was collected using an Isaacs-Kidd Midwater Trawl. Taxonomic analysis revealed 248 taxa of zooplankton belonging to 20 orders. Marked differences in taxa composition were observed between the Subtropical region of the Southern Indian Ocean and the Southern Ocean because of the significant influence of hydrological fronts, such as the Subtropical Front (STF) and the Subantarctic Front (SAF), in structuring zooplankton assemblages. These differences are due to the closeness of these fronts, notably North of Crozet, where a triple front is observed, and North of Kerguelen, where the transition between the Polar Frontal Zone (PFZ) and the Subtropical Zone (STZ) is narrow.

Résumé

Ce document étudie la répartition spatiale du macrozooplancton dans différentes régions hydrologiques dans la partie sud de l'océan Indien et dans l'océan Austral, englobant les archipels de Crozet et de Kerguelen situés dans l'océan Austral, ainsi que les îles de Saint-Paul et de Nouvelle Amsterdam dans le sud de l'océan Indien. Les données utilisées dans cette étude ont été recueillies lors des campagnes REPCCOAI menées pendant les étés 2017 à 2019 à bord du navire de recherche *Marion Dufresne II*. Le macrozooplancton a été collecté à l'aide d'un chalut pélagique Isaacs-Kidd. L'analyse taxonomique a révélé 248 taxons de zooplancton appartenant à 20 ordres. Des différences marquées dans la composition des taxons ont été observées entre la région subtropicale du sud de l'océan Indien et l'océan Austral en raison de l'influence significative des fronts hydrologiques, tels que le Front subtropical et le Front subantarctique (FSA), dans la structuration des assemblages zooplanctoniques. Ces différences sont dues à la proximité de ces fronts, notamment au nord de Crozet, où l'on observe un triple front, et au nord de Kerguelen, où la transition entre la Zone frontale polaire (ZFP) et la Zone subtropicale (ZST) est étroite.

Абстракт

В данной работе исследуется пространственное распределение макрозоопланктона в различных гидрологических регионах южной части Индийского океана и Южного океана, включая архипелаги Крозе и Кергелен в Южном океане, а также острова Сен-Поль и Новый Амстердам в южной части Индийского океана. Данные, использованные в данном исследовании, были собраны в ходе съемок REPCCOAI, проведенных летом 2017–2019 годов с борта научно-исследовательского судна *Marion Dufresne II*. Макрозоопланктон собирался с помощью разноглубинного трала Айзекса-Кидда (Isaacs-Kidd Midwater Trawl). Таксономический анализ выявил 248 таксонов зоопланктона, относящихся к 20 отрядам. Были отмечены заметные различия в составе таксонов между субтропическим регионом южной части Индийского океана и Южным океаном из-за значительного влияния гидрологических фронтов, таких как Субтропический фронт (СТФ) и Субантарктический фронт (САФ), на формирование зоопланктонных сообществ. Данные различия обусловлены близостью этих фронтов, особенно к северу от острова Крозе, где наблюдается тройная фронтальная структура, и к северу от острова Кергелен, где граница между Полярной фронтальной зоной (ПФЗ) и Субтропической зоной (СТЗ) является узкой.

Resumen

En este artículo se estudia la distribución espacial del macrozooplancton en varias regiones hidrológicas del Océano Índico Meridional y del Océano Austral, abarcando los archipiélagos de Crozet y Kerguelén en el Océano Austral, y las islas de Saint-Paul y Nueva Amsterdam en el Océano Índico Meridional. Los datos utilizados en este estudio fueron recopilados por las prospecciones REPCCOAI realizadas durante los veranos de 2017 a 2019 a bordo del BI *Marion Dufresne II*. El macrozooplancton se muestreó con una red de arrastre de media agua Isaacs-Kidd. El análisis taxonómico reveló 248 taxones de zooplancton, pertenecientes a 20 órdenes. Se observaron diferencias marcadas en la composición taxonómica entre la región subtropical del Océano Índico Meridional y el Océano Austral debido a la significativa influencia de los frentes hidrológicos, como el Frente Subtropical (FST) y el Frente Subantártico (FSA), en la estructuración de las agrupaciones de zooplancton. Estas diferencias se deben a la proximidad de estos frentes, especialmente al norte de Crozet, donde se observa un frente triple, y al norte de Kerguelén, donde la zona de transición entre la Zona Frontal Polar (ZFP) y la Zona Subtropical (ZTS) es estrecha.

Introduction

The French Southern and Antarctic Lands (TAAF), encompassing the Crozet Archipelago, the Kerguelen Islands and the Saint Paul and New Amsterdam Islands, are renowned for their unique marine ecosystems. These islands are located in two distinct oceans: the Southern Ocean and the South Indian Ocean. Each markedly having contrasting physico-chemical characteristics across a narrow latitudinal band. The South Indian Ocean is oligotrophic, characterised by warm and saline waters, while the Southern Ocean is noted for its colder waters and high nutrient concentrations. The subantarctic islands (Crozet and Kerguelen) and subtropical islands (Saint Paul and New Amsterdam) exhibit high chlorophyll concentrations due to the presence of island shelves that enhance primary production by enriching the environment with iron (Blain et al., 2007). These unique regional features make the French Southern Territories sanctuaries of biodiversity, supporting the entire food web through large biomasses of zooplankton and micronekton which includes small pelagic fish. Euphausiids are an essential intermediate trophic level taxon. They are abundant around these islands (Cuzin-Roudy et al., 2014) and serve as a crucial prey source for marine birds and mammals (Deagle et al., 2007; Xavier et al., 2017; Riaz et al., 2020). Other taxa such as amphipods play a similar role akin to euphausiids, being prey for fish and birds (Padovani et al., 2012; Riaz et al., 2020). Additionally, gelatinous organisms such as jellyfish, salps, and siphonophores are also abundant and play significant roles in the ecosystem functioning in both the Southern Ocean and the South Indian Ocean.

Despite the importance of these taxonomic groups, some microzooplankton taxa remain understudied. This is the case of gelatinous species for which few species are recorded in international databases. The Response of the pelagic ecosystem to climate change in the Southern and South Indian Oceans (REPCCOAI) surveys aim to address this by inventorying all macrozooplanktonic taxa present in the Southern Ocean between Crozet and Kerguelen and in the South Indian Ocean North of Crozet and from Kerguelen to New Amsterdam. These surveys were conducted from January and February 2017 to 2019 aboard the R/V *Marion Dufresne II* and sampled both macrozooplankton and micronekton from the epi- and mesopelagic zones using an Isaacs-Kidd Midwater Trawl (IKMT). The sampling network crossed several oceanographic and biogeochemical provinces (Figure 1).

The study area is separated by different hydrological fronts, identifiable by their physical and chemical characteristics. The Subtropical Zone (STZ) lies in the Northern part of the study area with the Subtropical Front (STF) marking its southern boundary. This zone includes the islands of Saint-Paul and New Amsterdam, as well as various ridge systems. The Subantarctic Zone (SAZ) is bounded by the STF to the north and the Subantarctic Front (SAF) to the south. The two fronts are close together in some areas, with notable differences observed around Crozet and Kerguelen. North of Crozet, a 'Triple Front' occurs where the Agulhas Return Current Front (ARCF), STF and SAF converge (Belkin and Gordon, 1996). North of Kerguelen, the STF, the SAF and the Polar Front (PF) are in close proximity. The PF lies far south of Crozet, near the Ob and Lena seamounts, and extends between Kerguelen and Heard and Macdonald Islands, continuing north-eastwards off the Kerguelen shelf where it intersects with the SAF and STZ (Gamberoni et al., 1982; Charriaud and Gamberoni, 1987; Park et al., 1991 and 1993a and 1993b). These unique oceanographic features create a narrow transition between the Indian Ocean and the Southern Ocean, resulting in a reduced SAZ in comparison with the rest of the Southern Ocean. This explains the spatial segregation of pelagic assemblages that are separated by these different fronts, and in particular by the SAF and the STF. This was observed in the study area for lanternfish (Koubbi, 1993; Koubbi et al., 2011b), where the SAF was identified as a major biogeographic barrier in the Indian sector of the Southern Ocean. Vereshchaka et al. (2021) found similar results for mesozooplankton where the STF, SAF and PF together influenced species richness and diversity.

Therefore, understanding the biogeography of zooplankton species is crucial for defining assemblages in relation to the abiotic environment and for investigating the distributions of species that are important for higher trophic levels. In this study, we used the hydrological regionalisation by Djian et al. (2025) to analyse differences in taxonomic composition and diversity between the regions identified by these authors. This regionalisation is based on vertical temperature and salinity profiles over the austral summers from 2010 to 2020.

The main objective of this study is to assess the importance of different hydrological zones on the spatial distribution of macrozooplankton in the epi and mesopelagic zones. This includes key species such as euphausiids and amphipods, which are prey for marine birds and mammals, as well as gelatinous plankton which serve as indicators of hydrologic regions. Additionally, this study provides a benchmark for future research on the effect of climate change on the pelagic fauna of subtropical and subantarctic high seas areas.

Methods

Macrozooplankton was collected using an IKMT, a standard pelagic trawl designed for sampling macrozooplankton and micronekton. The net has an overall length of 17 m and has a metal wing. It had an opening area of 7 m² and a mesh size that decreased from 3.5 cm at the net entrance to 0.5 cm near the cod end. The net was towed at a speed of 2 to 3 knots and deployed from the surface to various depths, primarily 200, 600 or 1000–1200 m depending on the location of the sampling station and sea conditions. Sampling took place at a total of 82 stations during January and February 2017, 2018 and 2019 (Figure 1). The survey area covered a geographical area from 50°E to 85°E and 27°S to 60°S. The sampling network was mainly in the oceanic zone, although it included some stations on the shelves of the different islands.

Once the samples were collected, they were fixed in 5% formalin seawater buffered to the pH of seawater with sodium tetraborate. At the lab, samples were split using a Motoda box (Motoda, 1959) to produce equal fractions. For each major taxonomic group, counts were conducted on the fraction containing more than 100 individuals of the taxon. Individuals were identified to the species level. However, damaged organisms were identified to the genus or family levels, but this was only done rarely. Abundances were calculated as the number of individuals per unit volume of filtered seawater, estimated by using two methods: (1) based on the distance travelled by the net and its opening, and (2) using flow meters to calibrate the calculations.

Taxonomic identification was performed using a binocular microscope and using various taxonomic guides and identification keys for euphausiids (Kirkwood, 1982; Boltovskoy, 1999), amphipods (Boltovskoy, 1999), salps (O'Sullivan, 1983; Boltovskoy, 1999), siphonophores (Boltovskoy, 1999), chaetognaths (O'Sullivan, 1982a; Boltovskoy 1999), decapods (Kirkwood,1983; Boltovskoy, 1999), and Scyphomedusae and Hydromedusae (O'Sullivan, 1982b and 1982c; Boltovskoy, 1999).

All statistical analyses were performed using R software (version 4.1.0, Core Team, 2021), and maps were generated using ArcGIS 10.5.1 software. Species or taxa diversity (H') was mapped using the Shannon and Weaver index and the Pielou index (J) for evenness (Hill, 1973). Correspondence analysis (CA, Legendre and Legendre, 2012) was

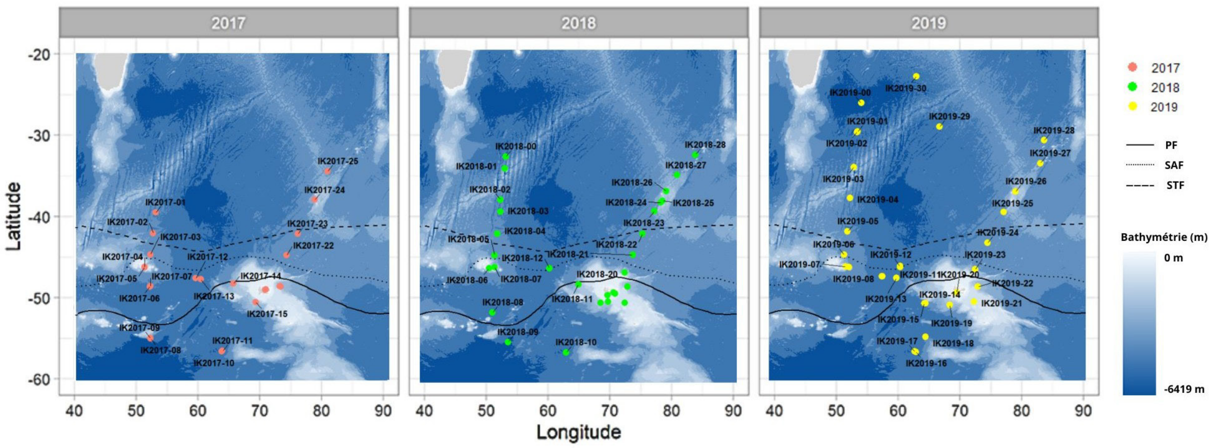

Figure 1: Maps showing the stations sampled during the REPCCOAI surveys in 2017, 2018 and 2019. The STF is represented by a solid line, the SAF by a dotted line and the PF by a dashed line. Stations codes are structured as follows: 'IK' for IKMT, '201X' for the year and a sequential number indicating the station's order during each survey

performed on the abundance data using the 'CA' function of the 'FactoMineR' package (Le et al., 2008) to analyse relationships between stations and taxa abundances. Abundances from 23 stations in 2017, 28 stations in 2018 and 30 stations in 2019 were analysed. Only taxa comprising more than 3% of the total abundance were included in the analysis, resulting in a dataset of 127 taxa. Station 'IK2018-4' was included as an additional observation due to the high abundance of one taxon present at this station. Abundance data were log-transformed to approximate normal distributions. Environmental variables were included as additional quantitative variables to aid in interpreting the CA. These variables were chlorophyll-a concentration (to distinguish productive from oligotrophic areas), Kinetic Energy (to identify turbulent areas), Mixed Layer Depth (MLD), Sea Surface Temperature (SST) and surface salinity. The environmental dataset is the same as the one used by Djian et al. (2025) from Copernicus. Djian et al. (2025) identified seven hydrological regions through functional Principal Component Analysis (fPCA) on temperature and salinity vertical profiles. Four regions are located in the Southern Indian Ocean (Tropical Zone, Eastern Subtropical Zone, Western Subtropical Zone and Subtropical Convergence Zone) and three in the Southern Ocean (Subantarctic Zone, Polar Frontal Zone and Antarctic Zone). The spatial distribution of oceanic fronts was confirmed by the standard deviation of these hydrological regions' spatial distribution aligning with the positions of the hydrologic fronts (Park et al., 1991). Additional details on these hydrologic regions are available in Table 1.

Table 1: Hydrologic regions and their characteristics defined by Djian et al. (2025).

Region number	Region's name	Code	Fronts/currents associated
1	Tropical Zone	TZ	South Equatorial Current
2	Eastern Subtropical zone	ESTZ	Indian Subtropical Gyre
3	Western Subtropical zone	WSTZ	East Madagascar Current
4	Subtropical Convergence Zone	STCZ	NSTF-SSTF
5	Sub-Antarctic Zone	SAZ	SSTF-SAF
6	Polar Frontal Zone	PFZ	SAF-APF
7	Antarctic Zone	AZ	APF

Results

Species diversity

A total of 248 zooplanktonic taxa (including 203 species) belonging to 20 orders were identified in the IKMT samples during the REPCCOAI surveys. These included 49 taxa of amphipods (42 species), 44 taxa of euphausiids (40 species), 52 taxa of siphonophores (43 species) and 14 taxa of salps (12 species). The remaining taxa belonged to hydrozoans, scyphozoans, chaetognaths, etc. The Shannon and Weaver indices (H') differ between the South Indian Ocean and the Southern Ocean (Figure 2). Values range from 3.4 to 2.7 north of the SAF, indicating high taxa diversity. The Pielou index J is also high in the subtropics, ranging from 0.7 to 0.83. This suggests that taxa are evenly distributed in terms of abundances. In the Southern Ocean, two categories of stations can be distinguished. The first category comprises those located in the PFZ, which exhibit low H' values between 1 and 2 and J values between 0.4 and 0.6. The second category comprises the remaining stations, which are situated in close proximity to islands. These stations exhibit the minimum observed values for both indices, indicating that the diversity is characterised by few dominant species. The Antarctic Zone (AZ) stations show more variability in H' (between 1 and 2) and J (between 0.4 and 0.6), indicating a lower diversity compared to the subtropical assemblages.

The euphausiids emerge as the most dominant group (Figure 3, indicated by the orange colouring), accounting for more than 95% of the plankton in some samples. Additionally, there is a strong contribution of amphipods in the samples south of the SAF (Figure 3, in green), where they can represent up to 90% of the plankton. Salps have a high contribution in the Southern Ocean (Figure 3, in yellow). Finally, siphonophores are abundant in the Indian Ocean (Figure 3, in pink).

Figures 4, 5, and 6 present the abundances of the most dominant species among amphipods (*Themisto gaudichaudii*, *Phronima sedentaria*), euphausiids (*Euphausia spinifera*, *Euphausia triacantha*, *Euphausia vallentini*, *Nematoscelis megalops*), salps (*Salpa thompsoni*), and siphonophores (*Chelophyes appendiculata*, *Nectadamas diomedeae*, *Rosacea plicata*), respectively. Certain species, such as *P. sedentaria*, *E. spinifera*, and *C. appendiculata*, exhibited higher abundances in the Southern Indian Ocean. In contrast, *T. gaudichaudii*, *E. vallentini*, *S. thompsoni*, and *R. plicata* are more prevalent in the Northern Indian Sector of the Southern Ocean.

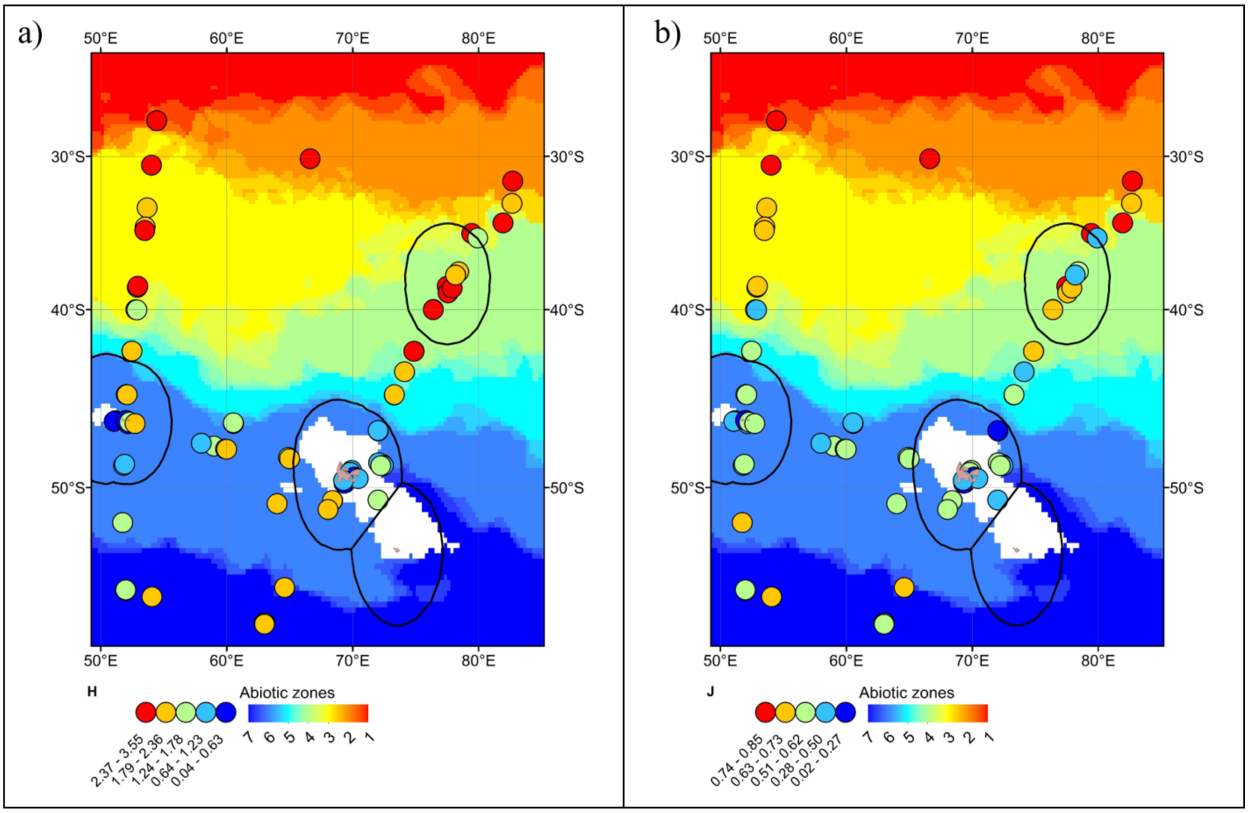

Figure 2: Mapping of a) the Shannon index and b) Pielou index of REPCCOAI samplings from 2017 to 2019. The hydrological regions identified by Djian et al. (2025) are shown.

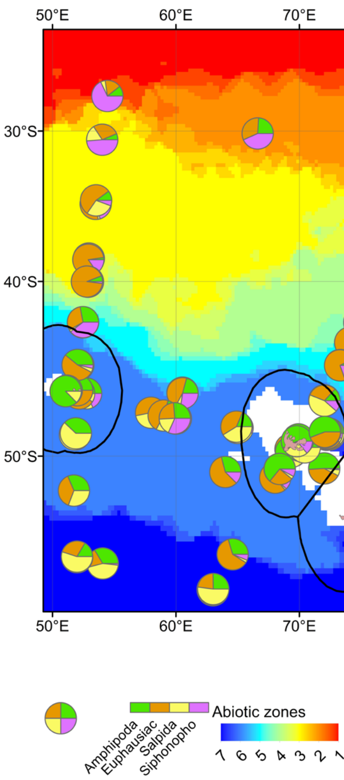

Figure 3: Mapping of relative abundances of taxonomic groups. The hydrological regions identified by Djian et al. (2025) are shown.

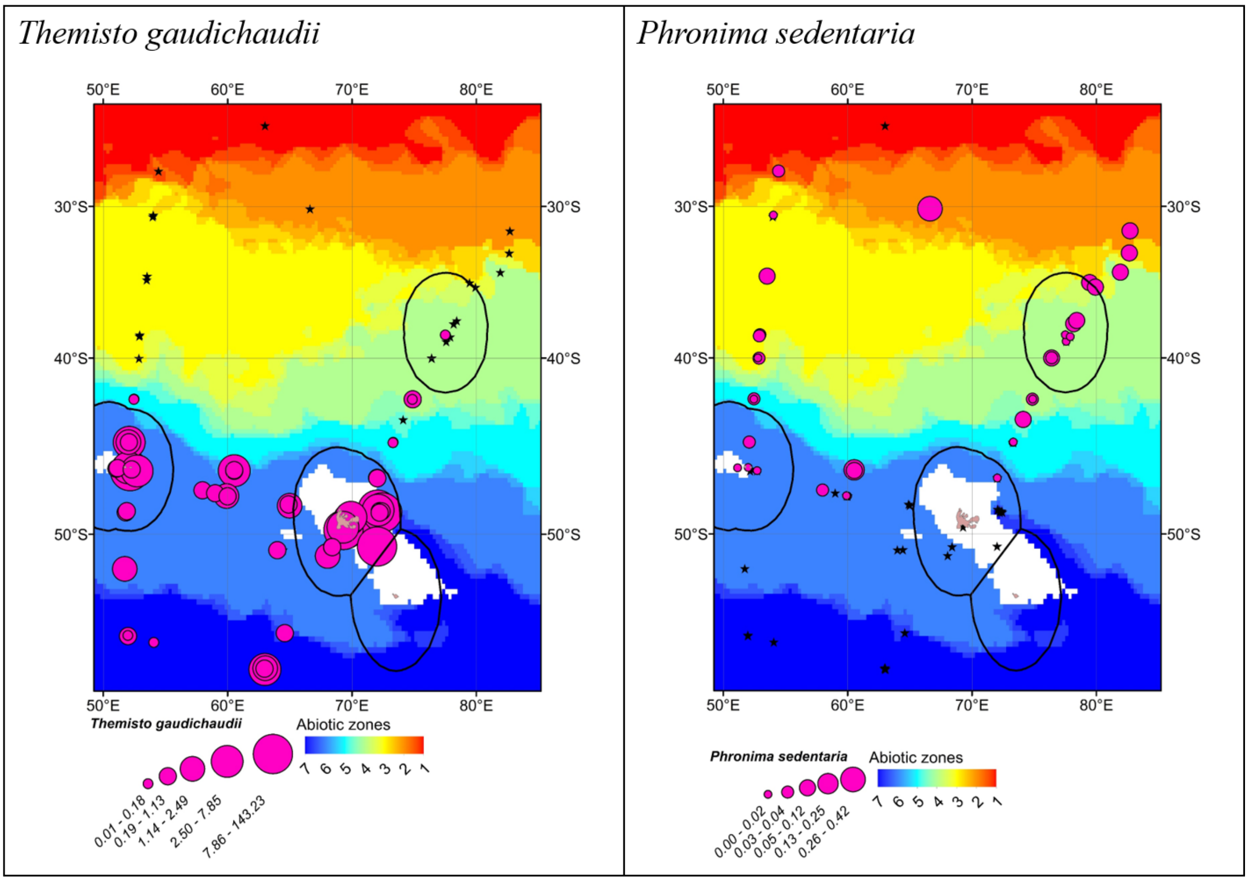

Figure 4: Maps showing the abundances (no. individuals/1000 m^3) of two amphipod species from the REPCCOAI surveys. The hydrological regions identified by Djian et al. (2025) are shown.

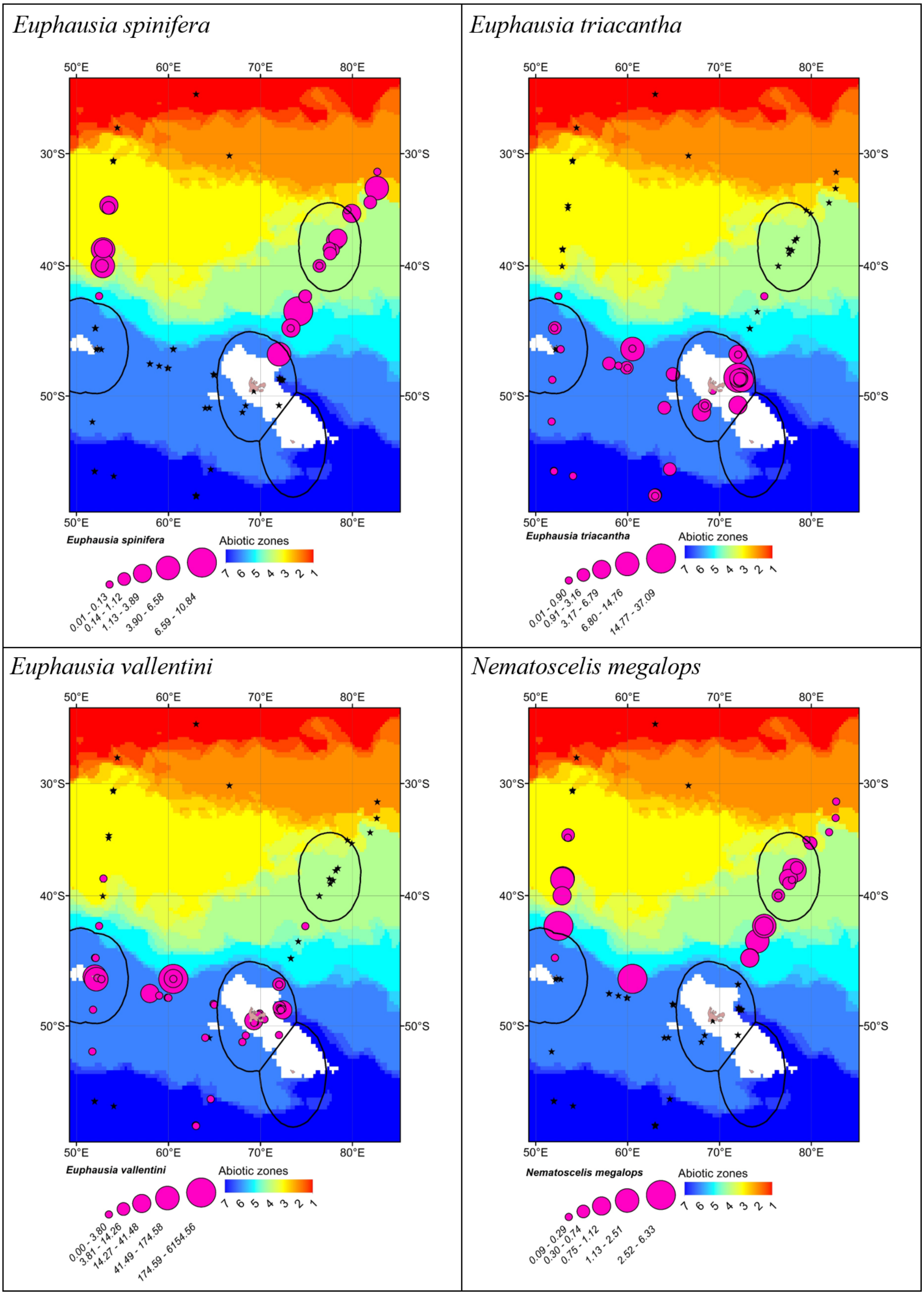

Figure 5: Maps showing the abundances (no. of individuals/1000 m^3) of four euphausiid species from the REPCCOAI surveys. The hydrological regions identified by Djian et al. (2025) are shown.

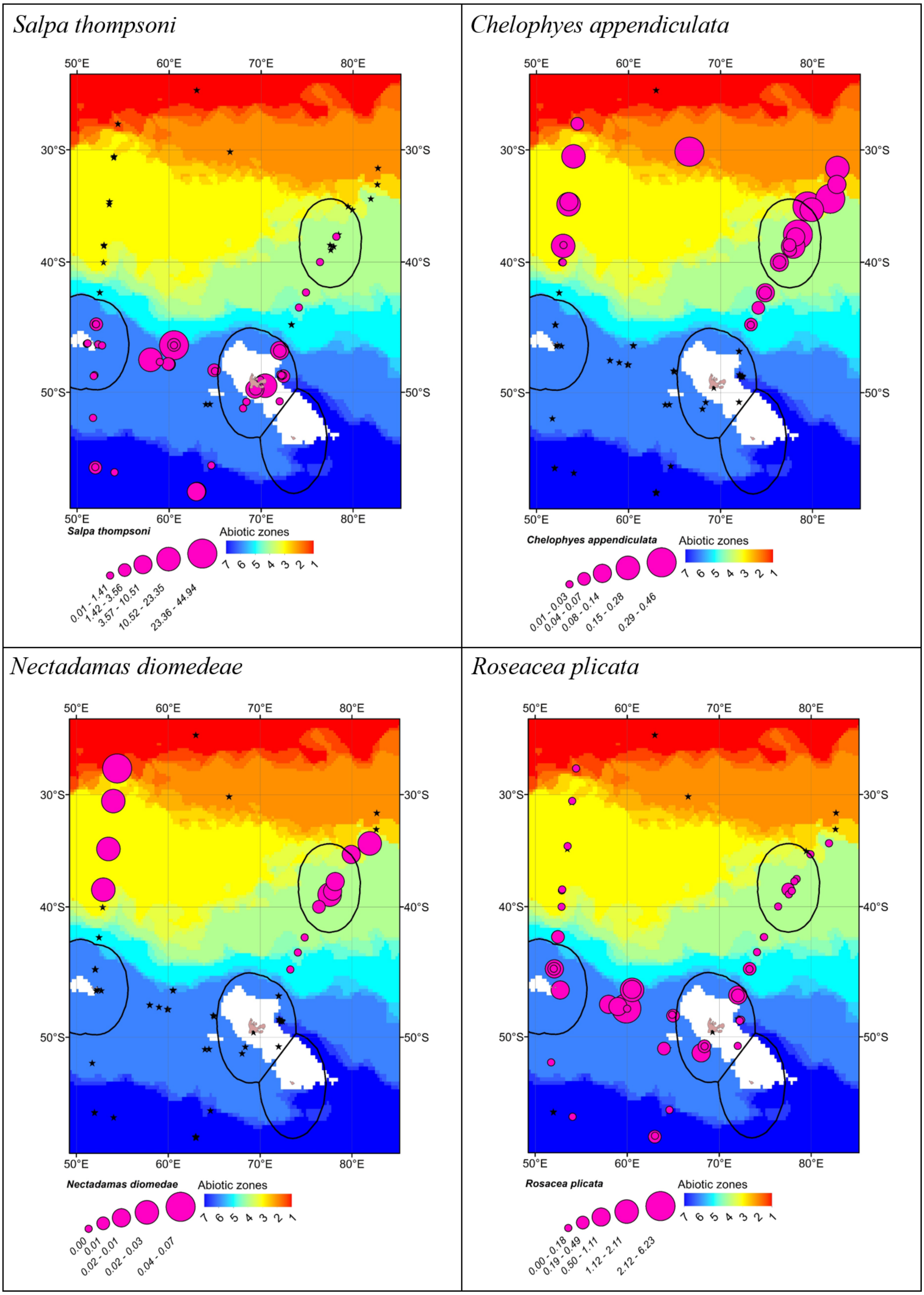

Figure 6: Maps showing the abundances (no. of individuals/1000 m*3*) of *Salpa thompsoni* (salp) and three species of siphonophores from the REPCCOAI surveys. The hydrological regions identified by Djian et al. (2025) are shown.

Correspondence Analysis

The first factorial axis of the Correspondence Analysis (CA) performed on abundances represents 19.5% of the total inertia, while the second axis represents 8.3%. The first factorial plane indicates a Guttman effect (Figure 7) due to a strong latitudinal gradient in the data. Indeed, it can be related to the hydrological regions described by Djian et al. (2025), and it can be observed that surface phosphate and chlorophyll-a concentrations are projected to the left of the first axis, while surface temperature and salinity are projected to the right of it.

The CA observation cloud (Figure 7) indicates that the Tropical Zone (TZ) stations contribute significantly to the first factorial axis, while the PFZ and AZ stations have a comparatively smaller contribution to this axis. A clear contrast can be observed between the TZ (in red), West STZ (WSTZ) and East STZ (ESTZ) stations (in orange and dark yellow) on the right of the first axis and the PFZ and AZ stations on the left (in green and blue).

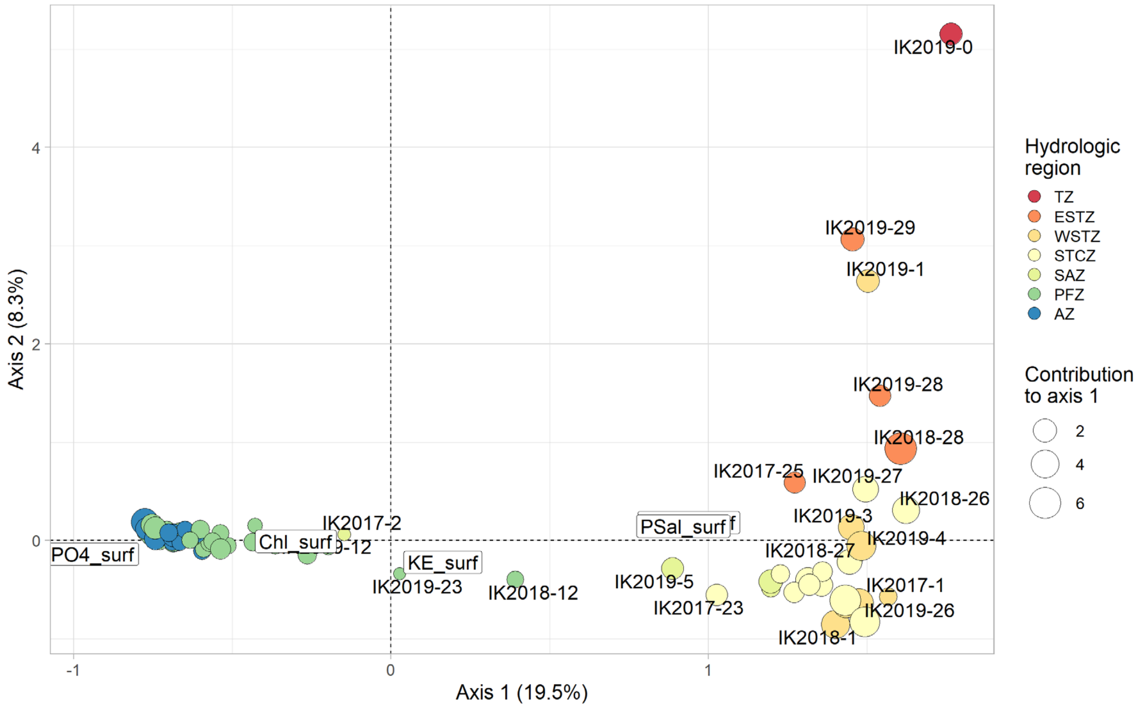

Figure 7: Barycentric representation of stations in the correspondence analysis factorial space. Point colour indicates hydrological regions identified by Djian et al. (2025) and point size is proportional to contribution to the first axis. Additional variables have been represented (PSal_surf as surface salinity, Temp_surf as surface temperature, KE_surf as surface kinetic energy, Chl_surf as chlorophyll-a surface concentration and PO4_surf as phosphate surface concentration).

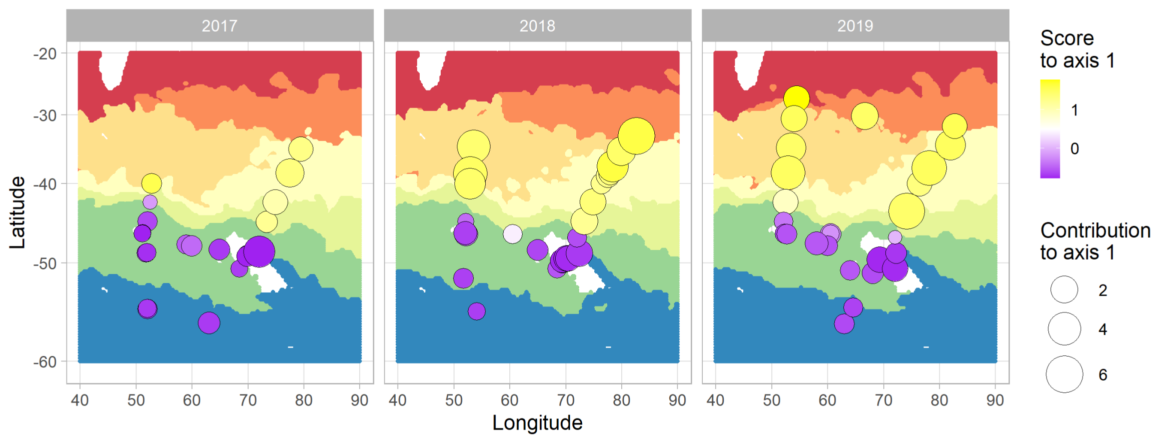

Figure 8: Mapping stations scores and contributions to CA axis 1. The hydrological regions identified by Djian et al. (2025) are shown.

The mapping of the scores and contributions of the first factorial axis reveals a clear separation at the level of the SAZ. The stations located to the north of the SAZ exhibit high scores and contributions to the first axis, in contrast to the lower scores and contributions observed for the stations situated to the south of the SAZ (Figure 8). The first axis allows for the differentiation of the cold, low saline, high nutrient stations of the PFZ and AZ from the warm, saline, low nutrient stations of the TZ, WSTZ, ESTZ and STCZ. The stations ‘IK2019-0’, ‘IK2019-1’ and ‘IK2019-29’, which are located to the north of the TZ, have the highest contribution to the second axis. This suggests that they represent a distinct tropical zone-taxa assemblage when compared to the rest of the sampling network (Figure 9).

Figure 10 illustrates the distribution of taxa along the first factorial axis. The species with the

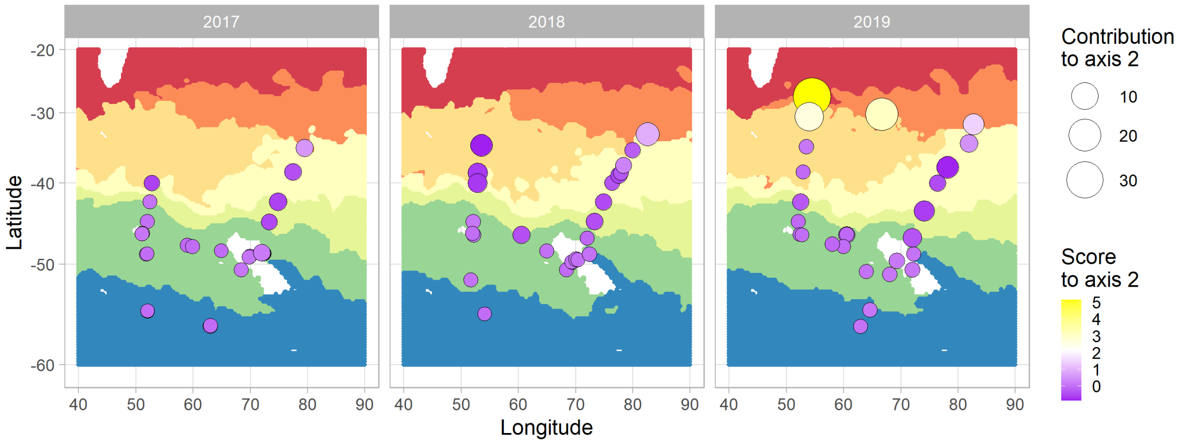

Figure 9: Mapping stations scores and contributions to CA axis 2. The hydrological regions identified by Djian et al. (2025) are shown.

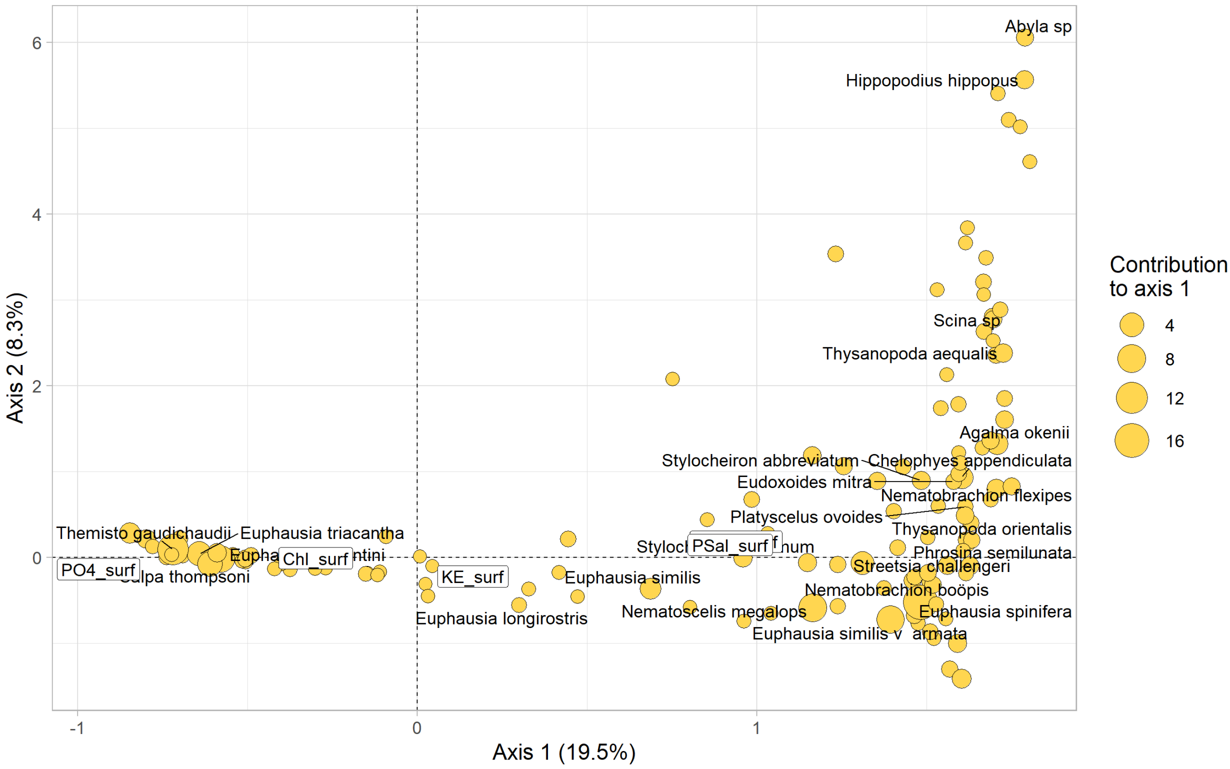

Figure 10: Barycentric representation of the taxa scatter plot in the CA factor space. Their size is proportional to their contribution to the first axis. Additional variables have been represented (PSal_surf as surface salinity, Temp_surf as surface temperature, KE_surf as surface kinetic energy, Chl_surf as chlorophyll-a surface concentration and PO4_surf as phosphate surface concentration).

greatest contribution to this axis are the euphausiids *Euphausia spinifera*, *Nematoscelis megalops*, *E. similis var armata* and the siphonophore *Chelophyes appendiculata*, which are located to the right of the axis. The euphausiids *E. vallentini*, *E. triacantha*, the amphipod *Themisto gaudichaudii* and *Salpa thompsoni* represent the species to the left of the first factorial axis. The taxa with the greatest contribution to the second factorial axis are the siphonophores *Hippopodius hippopus* and *Abyla sp.* The CA allows a first differentiation between 1) the planktonic assemblages in the PFZ and AZ, 2) those in the ESTZ, WSTZ and STCZ and 3) those observed in the TZ.

Discussion

Several marine surveys have previously documented zooplankton, such as the SKALP, SUZIL and ANTARES surveys conducted around Kerguelen or Crozet (Koubbi et al., 2011a; Koubbi et al., 2012). The SUZIL oceanographic survey in 1991 (Park et al., 1993b) was the first investigation on the biogeography based on fish larvae between Crozet, Kerguelen and New Amsterdam (Koubbi et al., 1993). Similarly, the SKALP surveys in 1987 and 1988 (Duhamel, 1993) focussed on fish larvae (Koubbi et al., 1991) and plankton distribution in the oceanic zone, as well as along the island shelf of Kerguelen, the Skif bank and the Kerguelen Heard seamounts (Koubbi et al., 2011b). In addition to SUZIL, the ANTARES surveys covered a broad latitudinal gradient from 43°S to 58°S but were conducted on a narrow longitudinal band (between 60°E and 65°E) (Mayzaud et al., 2002a and b).

These datasets, among others, were incorporated into the Biogeographic Atlas of the Southern Ocean (De Broyer et al., 2014), a comprehensive synthesis of the biodiversity of this ocean. Maps from historical explorations to the present day also integrate extensive data from initiatives like the International Polar Year (2007–2009) and the Census of Antarctic Marine Life – CAML (2005–2010). Findings from the Atlas regarding euphausiids (Cuzin-Roudy et al., 2014), fish (Duhamel et al., 2014) and hyperiid amphipods (Zeidler and De Broyer, 2014) indicate that the area around the Kerguelen Islands was quite well sampled. However, our understanding remains incomplete elsewhere due, for example, to the absence of data around Crozet Islands.

In the biogeographic atlas, certain taxa, such as salps, pelagic decapods, chaetognaths or non-hyperiid amphipods (Zeidler and De Broyer, 2014), lack comprehensive biogeographical coverage. While the atlas has described the latitudinal zonation of taxa in accordance with the three major fronts (the PF, the SAF and the STF), the pattern near Crozet and Kerguelen is unusual, compared to the rest of the Southern Ocean, due to the geographical proximity of some of these fronts. Additionally, the Agulhas Return Current Front is also influencing the western part of the study area North of Crozet. Recent studies were also carried out around subantarctic islands, notably around Heard and MacDonald islands – HIMI (Hunt and Swadling, 2021) and in the vicinity of the Prince Edward Islands archipelago – PEI (Stirnimann et al., 2021).

For the Indian Ocean, comprehensive samplings were conducted during the first International Indian Ocean Expedition (IIOE, Brinton and Gopalakrishnan, 1973), spanning from 1952 to 1965, and this effort continued with the second IIOE in 2015. Beyond these key research initiatives, other main studies have also been directed towards zooplankton in the South African oceanic zone (Gibbons et al., 1995; Gibbons and Thibault-Botha, 2002; Vereshchaka et al., 2021). However, when considering OBIS or GBIF data, the Subtropical Zone of our area of investigation reveals sparse records in our area of investigation North of Crozet or around St Paul and Amsterdam islands.

As the REPCCOAI surveys focused on the epi- and mesopelagic fauna of the oceanic zone, they did not sample intensively the neritic zone, and the coastal areas. These zones were the subject of previous surveys from the 1980s to 2000 and are summarized by Koubbi et al. (2011). Some of these surveys also aimed to study mesozooplankton and particularly copepods such as the coastal endemic species *Drepanopus pectinatus* or the main amphipod *Themisto gaudichaudii*. Concerning offshore mesozooplankton, additional studies, such as the work from Venkataramana et al. (2020) added new information on zooplankton diversity in the area of investigation of this paper. Nevertheless, certain taxa were either omitted from their analysis or identified solely at the family level. This was the case for gelatinous organisms, for which identification is a particular challenge due to the damage of these organisms during sampling.

In our study, almost all individuals were identified to the species level, including gelatinous organisms such as siphonophores and salps. However, certain taxa were less well identified due to their condition during capture (e.g. some jellyfish) or because they were less underrepresented in the samples collected by the IKMT, primarily due to its mesh size (e.g. copepods, chaetognaths or other mesozooplankton taxa).

The REPCCOAI surveys had provided a significant input in our understanding of the biogeography of macrozooplankton across the Southern Ocean and the Southern Indian Ocean. In this paper, the analyses performed on 127 taxa allows the differentiation of species assemblages based on hydrological zones as defined by Djian et al. (2025). Major significant differences in macrozooplankton assemblages were observed between the subtropical Southern Indian Ocean and the Southern Ocean.

Zooplankton in the Southern Indian Ocean

Throughout the REPCCOAI surveys, few tropical and the subtropical samplings were grouped together, indicating slight difference in taxa composition between these zones (Figure 7, red to yellow dots). These samples exhibited high taxa richness, diversity and evenness. These findings are consistent with the latitudinal diversity gradient, which shows peak values at the equator gradually decreasing towards the poles (Chaudhary et al., 2016).

In our study, euphausiids were the most abundant macrozooplankton group in the Southern Indian Ocean, with *E. spinifera*, *E. similis v. armata* and *N. megalops* standing out as the dominant species. These species are found in the vicinity of the SAZ and the STZ, which is consistent with observations from previous studies (Gibbons et al., 1995; Pakhomov et al., 1997; OBIS.org). They have an omnivorous diet, with a tendency towards carnivory in the chlorophyll-poor environment of the Southern Indian Ocean (Mayzaud et al., 2007).

During the surveys, we also noted a high abundance of siphonophores in the Southern Indian Ocean, comprising up to 50% of the total macrozooplankton collected. This high abundance is mainly due to the dominance of the species *Chelophyes appendiculata*, which is recognised to be one of the most abundant siphonophore species in the warm waters globally (Kirkpatrick and Pugh, 1984; Gusmão et al., 2015). Additionally, other species such as *Agalma okenii*, *Abyla trigona* and *Ceratocymba sagittata* are also prevalent in the Southern Indian Ocean (Boltovskoy, 1999; Thibault-Botha and Gibbons, 2005).

Furthermore, some differences in taxa composition were highlighted between the three northernmost stations within the Tropical Zone and the remaining stations across the Southern Indian Ocean. These stations are characterised by the presence of subtropical and tropical species, including some euphausiids such as *Thysanopoda obtusifrons*, *T. aequalis*, *T. pectinata*, *Stylocheiron carinatum* and *E. hemigibba*. These findings also show the existence of an East-West gradient in the taxonomic composition.

The study by Merland et al. (2025), which utilised climatic environmental parameters, revealed subdivisions between the eastern and western regions of the Southern Indian Ocean attributed to temperature differences. Previous studies have also documented these differences (Behera and Yamagata 2001; Suzuki et al. 2004; Morioka et al., 2010). This pattern is likely to be explained by the Agulhas Return Current, which transports warm waters from the low latitudes of the Indian Ocean towards the northern limit of the Southern Ocean. Consequently, this can potentially facilitate the introduction of species from more tropical waters into the western part of the Southern Indian Ocean.

Zooplankton in the Northern Indian Sector of the Southern Ocean

The Southern Ocean stations exhibited more homogeneous assemblages (Figure 10, green and blue dots) with low taxa diversity, consistent with findings by Chaudhary et al. (2016). The taxa diversity allows the differentiation between the PFZ and the AZ assemblages. Another contributing factor is the significance of island shelves within the PFZ, where two highly dominant species prevail: the euphausiid *E. vallentini* (Figure 8) and the amphipod *T. gaudichaudii* (Figure 7), both characteristic of the cold waters of this region. (Havermans et al., 2019). These species serve as the main prey for several species of planktivorous birds, including penguins (Hull, 1999; Deagle et al., 2007; Xavier et al., 2017), and are also prey for some mesopelagic fish (Padovani et al., 2012; Riaz et al., 2020). Additionally, the siphonophore *Rosacea plicata* is also characteristic of this region according to the literature (Panasiuk et al., 2020). Other species indicative of the Southern Ocean, such as the amphipod *Primno macropa* (Nelson et al., 2001) and the siphonophore *Vogtia serrata* (Pugh et al., 1997; Toda et al., 2014) are also present. Another important species associated with this region is the salp *S. thompsoni* (Figure 9), which exhibits high abundance in the PFZ in other subantarctic regions (Pakhomov and Hunt, 2017). Stations located south of the PF show a high contribution of *S. thompsoni* to the overall macrozooplankton abundance (Figure 6).

Conclusion

The findings of this study underscore the pivotal role of hydrological fronts in shaping macrozooplankton assemblages within the Southern Ocean and the Southern Indian Ocean. These results offer valuable insights into the ecological mechanisms governing oceanic ecosystems across both oceans. The marked differences observed between the subtropical waters of the Southern Indian Ocean and the polar waters of the Southern Ocean emphasise the significant influence of environmental conditions on the distribution and abundance of zooplankton species.

Frontal zones, notably the STF and the SAF, serve as critical boundaries, delineating habitats and influencing biotic interactions within the pelagic ecosystem. The taxonomic composition and species diversity variations observed along these hydrological gradients illustrate how organisms adapt to fluctuating environmental factors like water temperature, salinity, and nutrient availability.

These results are particularly relevant in the current context of climate change, where changes in the physico-chemical properties of the oceans are likely to have a significant impact on the distribution and abundance of marine species. Understanding these processes is imperative for evaluating how marine ecosystems respond to environmental stress and for informing conservation and management strategies aimed at safeguarding marine resources.

By incorporating these data into ocean prediction models, we can enhance our ability to forecast future changes in zooplankton distribution and abundance, as well as their impact on marine food webs and associated ecosystems.

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