Temporal and spatial variability in the mesozooplankton community off the Falkland Islands (Southwest Atlantic)

Rebecca Piontek [a],[*], Cornelia Jaspers [b], Maarten Boersma [c],[d], Alexander Arkhipkin [a]

[a] The Fisheries Department of the Falkland Island Government, Stanley, Falkland Islands
[b] Centre for Gelatinous Plankton Ecology and Evolution, DTU Aqua - Technical University of Denmark, 2800 Kgs. Lyngby, Denmark
[c] Alfred-Wegener-Institut, Helmholtz-Zentrum für Polar- und Meeresforschung, Biologische Anstalt Helgoland, Helgoland, Germany
[d] University of Bremen, FB2, Bremen, Germany

ABSTRACT

Zooplankton communities vary in space and time. Their composition is strongly influenced by lower trophic levels that are dependent on the availability of light and nutrients. As all marine ecosystems are relying on zooplankton as intermediate trophic step between primary production and higher trophic levels, changes in the zooplankton community composition and biomass can cascade through the food web with important impacts on fish communities and through that on fisheries yields. An intense fisheries exist around the Falkland Islands in the SW Atlantic Ocean, around 51° S, but to the best of our knowledge, no previous study has to date investigated the seasonal variation in zooplankton community composition in these waters. We show that copepods (39.2%), the larvae of the anomurid *Grimothea gregaria* (33.1%) and euphausiids (10.9%) dominate the local mesozooplankton community by biomass. All species showed seasonal patterns, including ontogenetic behaviour of *G. gregaria* migrating to deeper waters with development, which were significantly explained by temperature ($p < 0.001$). While overall biomass significantly decreased with distance from shore ($p < 0.001$), mesozooplankton diversity was highest at 30 km from shore. The presented study is the first assessment of the mesozooplankton biomass off the Falkland Islands and provides a first baseline to aid future ecosystem studies in the context of ecosystem based fisheries management in the region.

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1. Introduction

The Falkland Islands are located in the south-eastern part of the Patagonian Large Marine ecosystem (LME), which is one of the most productive marine ecosystems in the world (Arkhipkin et al., 2013; Lutz et al., 2018). Upwelling of nutrient rich Sub-Antarctic Water along the 200 m isobaths (Franco et al., 2008) on the shelf break in the southern part of the LME promotes primary production of up to 50 mg C m^{-3} h^{-1} in spring (Matano and Palma, 2008; Lutz et al., 2018). Warm water influxes from the northern parts of the shelf regions create extended oceanographic fronts, driving upwelling which is sustaining high quantities of phyto- and zooplankton in the Patagonian LME (Belkin et al., 2009). These fronts provide suitable spawning and feeding habitats for larvae and juveniles of various commercially relevant fish and squid species, including toothfish (*Dissostichus eleginoides*), Patagonian squid (*Doryteuthis gahi*) and Argentine shortfin squid (*Illex argentinus*) in the southern Patagonian LME (Bakun, 1993; Arkhipkin et al., 2013). Due to their commercial importance, research efforts so

far have been primarily devoted to ontogeny, migration pattern and feeding behaviour of those species (Chemshirova et al., 2021; Lee et al., 2021; Büring et al., 2022), while their main food source (mesozooplankton) has largely been neglected, especially around the Falkland islands.

Previous studies in other parts of the Patagonian LME have found a high zooplankton diversity, including 430 copepod species, 109 hyperiid amphipods and 31 euphausiids (Agnew, 2002; González et al., 2016; Cepeda et al., 2018). However, research has primarily focused on key mesozooplankton species e.g. *Themisto gaudichaudii* (Cepeda et al., 2018) and the wider mesozooplankton community has not been taken into much consideration. Generally, South Atlantic mesozooplankton communities are dominated by copepods accounting for over 70% of the total mesozooplankton abundances, followed by larvaceans (= appendicularians), hyperiid amphipods and euphausiids as additional contributors (Cepeda et al., 2018; Giménez et al., 2018). The spatial distribution of these genera was previously defined as stable within seasons in the Patagonian LME (Sabatini et al., 2016), however, other studies found that their abundance and biomass varied seasonally (Dias et al., 2015). Mesozooplankton abundance, sampled with a 200 μm net, may reach up to 60,000
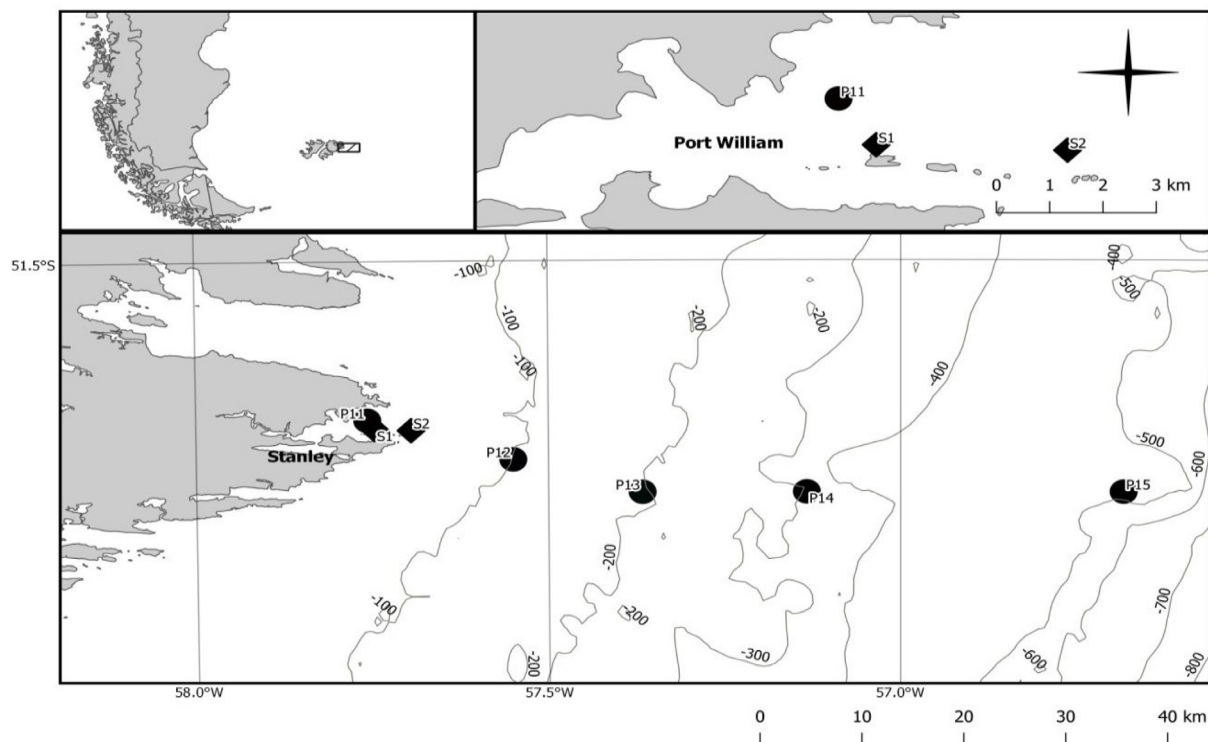
Fig. 1. Locations of sampling stations across the Patagonian shelf off the Falkland Islands. Mesozooplankton was collected monthly on board PV Protegat (●) and biweekly on board RV Jack Sollis (♦) during August 2020 to January 2022. Depth contours are indicated by 100 m isobaths.

ind m^{-3} in shallow depths, with typical counts above 20,000 ind m^{-3} in northern parts of the Patagonian LME (Miyashita et al., 2009; Dias et al., 2015). Nevertheless, in deeper, offshore regions of the Patagonian Shelf abundances were found to be under 5000 ind m^{-3} on average (Dias et al., 2015). Comparing abundance data of similar mesh nets across seasons, mesozooplankton densities increased by approximately 400% in summer compared to winter; followed by abundance and biomass decreases in late summer (Sabatini et al., 2012; Thompson et al., 2013; Sabatini et al., 2016; Cepeda et al., 2018).

Seasonal and spatial dynamics of mesozooplankton in Falkland Island waters remain poorly investigated. A study of zooplankton around the Falkland Islands identified multiple mesozooplankton species (i.e. *Euphausia lucens, Euphausia valentini, Grimothea gregaria, T. gaudichaudii*; Tarling et al., 1995). These species are common representatives of the southern part of the Patagonian LME, and provide an important feeding resources for several commercially relevant species (Guerrero et al., 1999; Cheung and Pitcher, 2005a; Nogueira and Brandini, 2018). However, in this area mesozooplankton has been studied primarily as prey items for fish and squid, such as rock cod (*Patagonotothenid* sp.), toothfish (*Dissostichus eleginoides*) or Patagonian squid (*Doryteuthis gahi*; Laptikhovsky and Arkhipkin, 2003; Arkhipkin et al., 2003; Büring et al., 2022) and, to our knowledge, no study investigated the local mesozooplankton community structure and its seasonal dynamics. Therefore, it is necessary to focus more research on mesozooplankton, especially in the light of high fishing pressures and changing environmental conditions.

The aim of the present study was to identify seasonal and spatial distribution and biomass pattern of the mesozooplankton community around the Falkland Islands. It is the first investigation focusing on mesozooplankton dynamics in Falkland Island waters and will be an important contribution to future ecosystem studies supporting ecosystem based fisheries management around the Falkland Islands.

2. Methods

2.1. Sampling

Mesozooplankton samples were collected monthly at 5 stations along the oceanographic transect 'P1' (Arkhipkin et al., 2004) by the fisheries patrol vessel *Protegat* between August 2020 and January 2022 (Fig. 1). Transect stations were located east of Port William covering water depths of 20, 100, 200, 300 and 500 m. A large bongo net (60 cm in diameter with two different mesh sizes of 500 and 350 μm) was used to perform vertical tows, integrating over the entire water column from the near bottom layers to the surface. Collected plankton samples were immediately frozen on board to avoid predation within the sample and to preserve the sample for later analysis on land. Over the course of the 1.5 year sampling period, 10 trips were conducted. During four sampling trips, not all stations could be sampled due to unfavourable weather conditions (Table 1).

A different sampling approach was utilized for two additional coastal stations that were sampled fortnightly in Port William using a small vessel *Jack Sollis*. At these stations, a smaller bongo net (30 cm in diameter with the same mesh size in both net ends of 350 μm) was used and towed horizontally for 10 min. Water depths at both stations ranged 20–30 m, however, samples were only collected from the surface water layer. Start of sampling was timed with incoming tides to reduce the influence of tidal mixture. Because there is no freezing capacity on board *Jack Sollis*, all samples were immediately fixed with buffered formaldehyde, with a final concentration of 4%. Despite the different sampling methods for harbour and transect stations, results were considered comparable as (1) the filtered water volumes per net were in general similar between both methods and (2) total mesozooplankton abundance collected in 350 and 500 μm meshed nets were comparable. Further, analyses of both preservation methods did only differ minimal in the total amount of mesozooplankton

Table 1

Sampling events with average water volume filtered and sampling events grouped into 7 investigation periods over 18 month. FV_H = water volume, horizontal tows; FV_T = water volume, vertical tows.

Investigation period	Dates	Harbour stations		Transect stations	
		# of samples	FV_H [m^3] $\pm$ SD	# of samples	FV_T [m^3] $\pm$ SD
Winter 20	August 2020	3[a]	30.2 $\pm$ 11.5	0	–
Spring 20	September–November 2020	12	134.5 $\pm$ 94.8	11[a]	63.85 $\pm$ 55.4
Summer 20/21	December 2020–February 2021	11[a]	51.6 $\pm$ 14.4	15	63.3 $\pm$ 48
Autumn 21	March–May 2021	12	44.6 $\pm$ 2.3	5	63.3 $\pm$ 49.8
Winter 21	June–August 2021	14	44 $\pm$ 1.6	5	63.3 $\pm$ 49.8
Spring 21	September–November 2021	12	42.2 $\pm$ 3	4[a]	43.8 $\pm$ 31.8
Summer 21/22	December 2021–January 2022	6	44.2 $\pm$ 2.5	5	63.3 $\pm$ 49.8

[a]Not all stations were sampled due to inclement weather.

Table 2

Length-weight-correlation with size range (mm) and wet weight range (mg). Non-linear regressions were used to obtain intercepts (a), slopes (b), R^2 and p-values of the regressions for all species and groups. For *Spongiobrachea australis* and ophiuroidae no regression was performed due to scarcity of data (n $\leq$ 5).

	n	Size range [mm]	WW range [mg]	Intercept (a)	p-value (a)	Slope (b)	p-value (b)	R^2	p-value
Primno sp.	20	0.5–12	0.6–9.8	0.00024	0.003	1.472	<0.001	0.845	<0.001
Themisto gaudichaudii	20	0.9–30	2–24	0.00095	0.009	0.901	<0.001	0.836	<0.001
Amphipoda	20	0.4–12.4	0.6–4.8	0.0006	<0.001	0.695	<0.001	0.752	<0.001
Copepods	20	1.1–3.4	0.1–0.4	0.00007	<0.001	1.355	<0.001	0.796	<0.001
Grimothea gregaria	20	0.9–17	0.6–6.7	0.00043	<0.001	0.942	<0.001	0.860	<0.001
Brachyura	20	1.4–9.1	0.1–7.1	0.00003	<0.001	2.41	<0.001	0.978	<0.001
Euphausia lucens	20	2.9–34.5	5.4–78	8.704E–07	0.288	3.227	<0.001	0.690	<0.001
Thysanoessa macrura	20	2.8–11.9	0.6–5.7	1.998E–06	0.319	3.183	<0.001	0.626	<0.001
Euphausiid	20	2–9.8	0.1–1.7	0.00005	0.056	1.43	<0.001	0.863	<0.001
Mysidacea	20	1.8–11.2	0.3–1.3	0.00003	0.007	1.528	<0.001	0.592	<0.001
Ostracoda	20	0.4–1.7	0.3–0.8	0.00028	<0.001	1.924	<0.001	0.364	0.003
Isopoda	14	1.8–6.5	0.1–0.5	8.853E–07	0.218	3.366	<0.001	0.248	0.040
Sagitta sp.	20	5.2–30.3	0.7–9.4	0.00001	0.027	2.028	<0.001	0.770	<0.001
Bivalvia larvae	20	2–3.1	8.3–23.2	0.00095	<0.001	2.811	<0.001	0.901	<0.001
Limacina helicina	20	0.3–2	0.3–1.7	0.00061	<0.001	1.298	<0.001	0.719	<0.001
Creseis sp.	20	0.3–2.1	0.1–1.6	0.00046	<0.001	0.88	<0.001	0.642	<0.001
Spongiobrachea australis	5	20.8–22	57.3–59.3	–	–	–	–	–	–
Cubozoa	20	3–16.6	0.7–3.8	0.00008	0.022	1.307	<0.001	0.835	<0.001
Ihlea magalhanica	20	48–103	1248–5901	0.00006	0.222	2.459	<0.001	0.881	<0.001
Polychaeta	20	2–22.9	0.7–4	0.00032	<0.001	0.743	<0.001	0.880	<0.001
Ophiuroidea	3	20.9–22.3	3.2–6.9	–	–	–	–	–	–
Fish larvae	20	4.3–38.1	0.8–28	0.00002	<0.001	1.960	<0.001	0.920	<0.001

(0.8%) or number of taxonomic groups (6%) caught per sample. Therefore, no differentiation between methods was made in the analysis and the samples from both net ends were pooled.

Main plankton groups and species were identified in the Falkland Islands Fisheries Department (FIFD) laboratory following taxonomic identification keys by Boltovskoy (1999). Identification and abundance estimations were conducted using an Olympus SZX12 dissecting microscope, with magnifications between x10 and x40 and an Olympus BX51 fluorescent microscope (magnification x100). In case of large amounts of individuals (more than 1000) of one species or taxonomic group after sorting, a subsample of 25% of the corresponding group was counted.

2.2. Mesozooplankton biomass and diversity

At least 5 individuals per taxonomic group were measured from each sample to calculate average size per taxonomic group. Additionally, for 20 individuals of each group total body length (L) and wet weight (WW) was measured over the whole sampling period to obtain length-weight-correlations (Table 2) following Eq. (1) for a nonlinear regression (Nakamura et al., 2017).

$$WW = a \times L^b \tag{1}$$

For horizontal tows at the harbour stations, the filtered water volume (FV_H) was calculated using trawling speed (s), trawl duration (t) and radius of the net (r, Eq. (2)). For vertically deployed nets during transect samplings, water volume (FV_T) was assessed by deployment depth (h) and radius of the net (r, Eq. (3)).

$$FV_H = (t \times s) \times \pi \times r^2 \tag{2}$$

$$FV_T = (h) \times \pi \times r^2 \tag{3}$$

The number of organisms for each taxonomic group per sample were divided by the volume filtered to estimate volume specific abundances per m^3. Abundance data were converted to biomass by using the generated length − wet weight (WW) relationships. Mesozooplankton diversity was assessed using the Shannon-Index (Shannon and Weaver, 1949), where low number represent a low diversity and high numbers represent high diversity.

For analysis and visualization R Studio (R version 4.0.2, RStudio Team, 2020) was used. Data was grouped into 7 investigation periods, based on season, to compensate for missing data from transect samples as outlined in Table 1.

Distance from shore for each station was calculated with the geosphere package (version 1.5–14; Hijmans, 2021) using the distHaversine function. Despite the different sampling techniques, stations with a distance from shore under 10 km (S1, S2 and P11) were considered 'nearshore stations' and stations over 10 km distance (P12–P15) as 'offshore stations'. Between sampling events, weekly diversity data per kilometre transect were extrapolated using the Hmisc package and a linear function (version 4.5-0; Harrell and Dupont, 2019). First, data were extrapolated in temporal direction to weekly data points prior to a second extrapolation over the distance to create a data point per

kilometre distance from shore. Those extrapolated data points were exclusively used for visualization without further statistical evaluations.

2.3. Correlation with environmental variables

Environmental variables i.e. potential sea temperature, sea surface salinity (SSS), chlorophyll *a* (chl *a*) and pH for the period 20th of August 2020 to 19th of January 2022 were retrieved from Copernicus Marine Environmental Monitoring Service on 29th of April 2022 (CMEMS, http://marine.copernicus.eu/). Potential sea temperature was derived from satellite sea surface temperature measurements and further referred as SST. SST (SD 0.5 °C) and SSS (SD 0.1) were extracted from GLOBAL_ANALYSIS_FORECAST_ PHY_001_024 product. For chl *a* (SD 0.1) and pH (SD 0.006) the product GLOBAL_ANALYSIS_FORECAST_BIO_001_028 was used. Data were retrieved for each sampling day, using the average sampling depth per station (Table A.1).

Spatial and seasonal variability in biomass and diversity were analysed per station over all seasons performing generalized additive models (GAMs) using the mgcv package (version 1.8–36; Wood, 2017). To investigate biomass and diversity, a GAM with a Gaussian distribution was used (León et al., 2008; Zuur, 2012). Biomass (B) and diversity (H') were modelled using distance from shore, SST, SSS, chl *a* and pH as continuous, season (4 level factor) and the interaction between the factors as explanatory variables. Both GAMs used an identity link function. Backwards model selection was performed on models with all combinations of explanatory variables, including all relevant interactions. When variables and interactions did not have a significant influence on the model and the model excluding the variable or interaction presented a lower Akaike information criterion (AIC), the variable and/or interaction was excluded from the model. In GAMs, we used the ti() function to model smooth terms for continuous variables. The ti() function creates a tensor product interaction smoother, which allows for the estimation of the interaction between two continuous variables, the main effects are to be included separately from the tensor product interaction (Zuur et al., 2009; Wood, 2017). The best fitting GAM with the lowest AIC did not contain pH and season with the interaction between temperature and chl *a* remaining as explanatory variables for biomass (Eq. (4)). For the diversity GAM, the most parsimonious model included all explanatory variables (Eq. (5)).

$$
\begin{aligned}
Biomass \sim{} & s(distance, k = 4) + s(SST, k = 4) + s(chl\ a, k = 4) \\
& + s(SSS, k = 4) + ti(distance, SST) + ti(distance, SSS) \\
& + ti(SST, SSS)
\end{aligned}
\tag{4}
$$

$$
\begin{aligned}
H' \sim{} & s(distance, k = 4) + s(SST, k = 4) + s(chl\ a, k = 4) \\
& + s(SSS, k = 4) + s(ph, k = 4) + ti(Distance, SST) \\
& + ti(SST, chl\ a) + ti(distance, SSS) + ti(distance, ph) + Season \\
& + f(SST) : Season + f(chl\ a) : Season
\end{aligned}
\tag{5}
$$

3. Results

3.1. Community composition

Copepoda were the main component of the mesozooplankton community, representing on average 39.2% of the biomass (Fig. 2). Further, *Grimothea gregaria* (33.1%), combined euphausiids (11%; *Euphausia lucens* 7.3%, *Thysanoessa macrura* 2.6%, unidentified euphausiids 1.1%), *Themisto gaudichaudii* (6.5%) and *Sagitta* sp. (4.4%) were major biomass contributors during the investigation period.

Grimothea gregaria was found to be at one prezoea and various larval stages (identified after Roberts, 1973) over the study period and locations. No mature or adult individuals were collected.

All stages were combined under *G. gregaria* and will hence be referred to as these.

All other taxonomic groups and species contributed to less than 2% of the overall mesozooplankton biomass each and included: Ophiuroidea, Cubozoa, *Creseis* sp. and *Spongiobrachea australis*. Mysidacea, Isopoda, *Ihlea magalhanica*, Ophiuroidea, *Creseis* sp. and *Spongiobrachea australis* only sporadically occurred. Common mesozooplankton groups and species such as copepods, *G. gregaria* and *T. macrura* were found more frequently and at higher densities at nearshore stations, while rare groups/species (<0.1%) were exclusively found at offshore stations (Table B.1). It is acknowledged that our sampling protocol and preservation technique likely underestimated the diversity and abundance of fragile mesozooplankton groups such as larvaceans, ctenophores and hydrozoan jellyfish.

3.2. Mesozooplankton biomass

Body lengths displayed large variations for *G. gregaria, T. gaudichaudii* and unidentified amphipods (Table 2). In contrast length variation was minimal for *Spongiobrachea australis*, Ophiurioidea and Bivalvia larvae (<20% of average length). The weight showed highest variations for unidentified decapoda, fish larvae and *T. gaudichaudii*. The regression showed a significant fit of the slope (p < 0.001) for all groups except Ostracoda and Isopoda. No regression could be performed for *Spongiobrachea australis* and Ophiuroidea due to scarcity of data.

Different seasonal patterns in mesozooplankton biomass (WW) were observed between nearshore and offshore stations. Biomass at stations S1, S2 and P11 (nearshore; Fig. 3) peaked in October–November 2020. A low biomass in March–May 2021 was followed by a slow increase in August–December 2021 with a short peak in August 2021 with a maximum of 10.2 g m^{-3}. On the contrary, offshore stations (P12–P15) started with a low biomass in September–November 2020 (>1.5 g m^{-3}) before plankton bloomed in December 2020–February 2021 over all outer stations with abundances of up to 2.5 g m^{-3} at station P14. This peak was followed by a slow decrease in biomass towards June 2021 (0.003 g m^{-3}) before a slight increase towards November 2021 at all offshore stations was observed. Nevertheless, average mesozooplankton biomass did not reach the same level in 2021/2022 compared to 2020/2021 (Fig. 3).

Copepods represented a major proportion of the overall biomass (39.2%) followed by *G. gregaria* (33.1%). Hence, their abundances drove the overall seasonal pattern. In detail, copepod biomass peaked in September–November in both sampling years but did not reach the same maximum in 2021 as 2020 (max in September 2020 = 3.6 g m^{-3}; November 2021 = 1.9 g m^{-3}). Similarly, chaetognaths peaked in September–October 2020. After lower biomass in December 2020–February 2021 over all stations, biomass increased towards June 2021. For *G. gregaria* a bloom was observed over two months (October–November 2020; max = 6.6 g m^{-3}) at all locations prior to a near absence in the water column until a smaller peak the following August 2021. *T. gaudichaudii* was found throughout the whole sampling period. Except from rarer occurrence in May–August 2021 at outer stations, specimens were sampled over all seasons and distances, peaking in April 2021 (max = 1.2 g m^{-3}) and rising biomass towards December 2021 and 2022. Contrary to these species, euphausiids displayed only one peak in biomass during the sampling period: Biomass was high in December 2020–February 2021 (max = 1.7 g m^{-3}), dominated by larger individuals found at offshore stations.

Biomass differed seasonally between the two location types. Overall, mean biomass was higher and more variable at nearshore stations (1.03 g m^{-3}, min = 0.001 g m^{-3}, max = 10.2 g m^{-3}) compared to offshore stations (0.7 g m^{-3}, min = 0.001 g m^{-3},
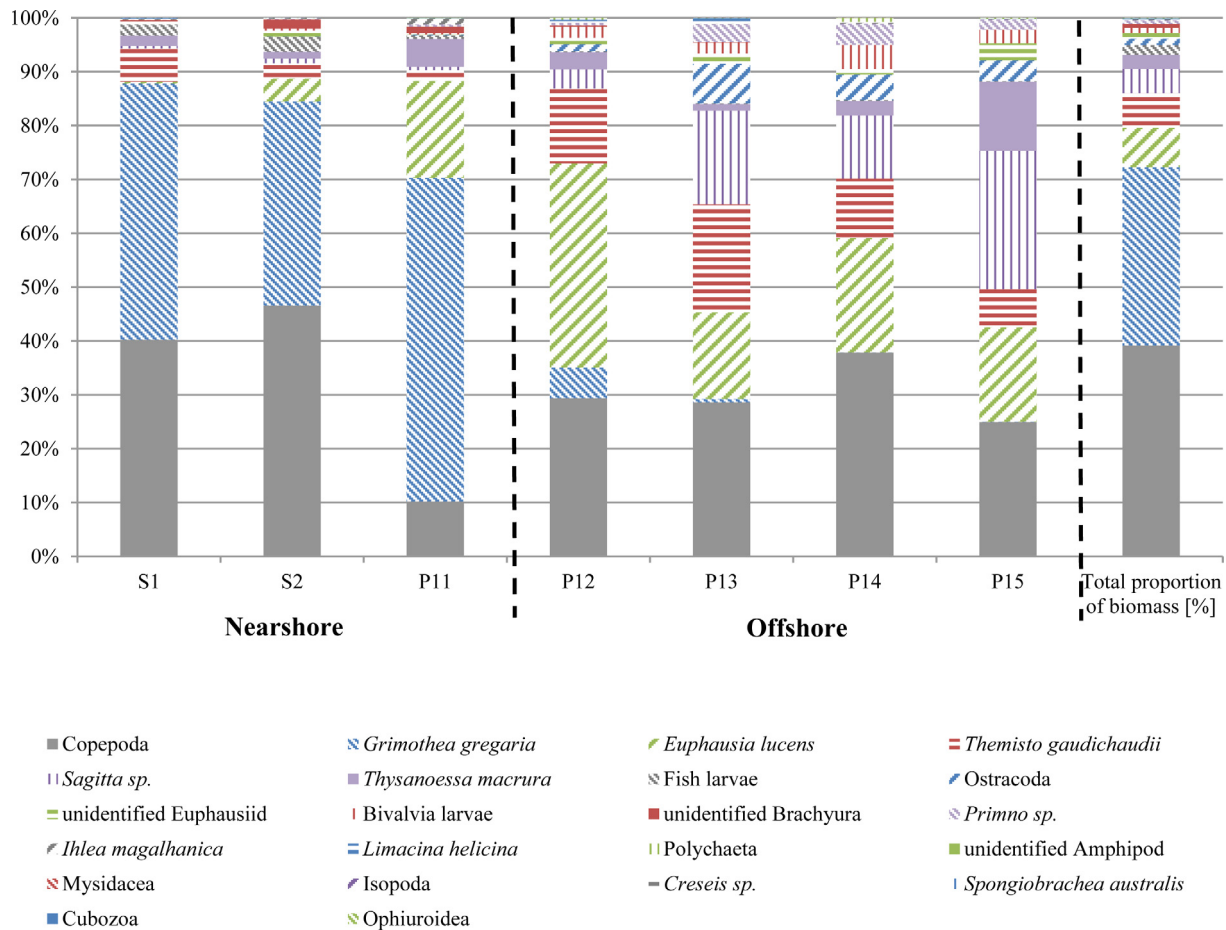
Fig. 2. Average percentage of biomass per group for each station. Nearshore stations = S1, S2, P11; offshore stations = P12, P13, P14, P15. Total proportion of biomass represents the average contribution of each group i.e. species over all stations.

max = 2.5 g m^{-3}) with total mesozooplankton biomass slightly decreasing with increasing distance from shore (Fig. 3). Similar spatial distributions were observed for copepods, with decreasing biomass offshore (average nearshore = 0.4 g m^{-3}; offshore = 0.2 g m^{-3}). A higher *G. gregaria* biomass was found nearshore (0. 37 g m^{-3} on average), decreasing with distance from shore to very low biomass 20 km offshore (>0.005 g m^{-3}). Contrarily, higher abundances of chaetognatha were found with increasing distance from shore (average = 0.1 g m^{-3}, max = 0.7 g m^{-3}), compared to samples closer to shore (average = 0.1 g m^{-3}, max = 0.68 g m^{-3}). The same applied to euphausiids, with higher biomass offshore (nearshore = 0.05 g m^{-3}; offshore = 0.2 g m^{-3}). Similarly, *T. gaudichaudii* was generally more abundant at offshore stations (average offshore = 0.1 g m^{-3}; nearshore = 0.07 g m^{-3}), however, highest biomass was measured at 29 km distance from shore (P13) with 0.15 g m^{-3}.

3.3. Mesozooplankton diversity

At nearshore stations (S1, S2 and P11) no seasonal diversity (H') trends were observed. However, at offshore stations (P12–P15), diversity varied with season (Fig. 4). At offshore stations, the sampling period started with a diversity peak in August/September 2020 (>2), which was followed by a decrease throughout the rest of the seasons, until a second diversity peak was observed during August–October 2021. Despite an observed seasonal cycle of diversity, the range of diversity varied interannually with slightly lower maxima in 2021 (1.7 in P12, 2 September 2021) compared to 2020 (1.8 in P13, 3 September 2020).

Apart from the seasonal trends (as presented above), spatial diversity of the mesozooplankton community displayed high variability along the transect. The average Shannon diversity index (H') across all stations was 0.6. However, offshore station showed a higher average H'-index of 0.9 compared to nearshore stations with an average of 0.4, due to a diversity peak at 29 km from shore. Nearshore stations (S1, S2 and P11) did not display H' over a maximum of 1.5 across the entire sampling period (14 December 2020 in P15). In contrast, H' at offshore stations reached up to 1.85 during the sampling period (3 October 2020 in P13), displaying a higher variability throughout the year.

3.4. Correlation with environmental variables

Sea surface temperature (SST) ranged between 4.1 °C to 11.6 °C (Fig. 5). Across all stations and seasons, average SST was 7.2 °C ± 2.3. Highest SSTs were reached during January–March. The first summer (December 2020–February 2021) was on average 1 °C warmer than the following year. Overall, the SST decreased with increasing distance from the Falkland Islands (average station S1 = 7.8 °C, P15 = 5.1 °C).

Highest chl *a* values were found in November 2021 (2.4 mg m^{-3}) and lowest during September 2021 (0.2 mg m^{-3}). In general, higher chl *a* concentrations were found in September–February (1.07–2.36 mg m^{-3}) compared to March–August (0.31–0.51 mg m^{-3}) in both years. Chl *a* followed a comparable spatial pattern with higher values at nearshore stations (e.g. maxima of 2.5 mg m^{-3} in 2020 at station P11).
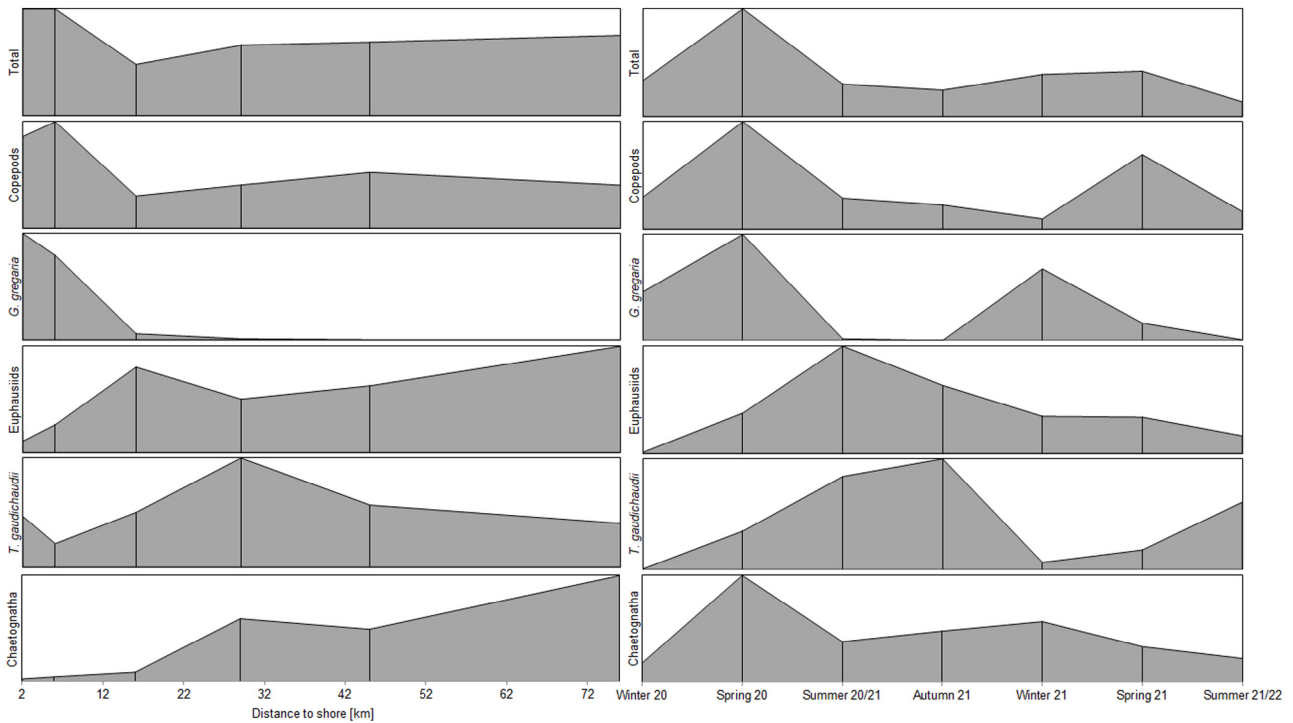
Fig. 3. Geographic (left) and seasonal (right) patterns of mesozooplankton biomass (WW), normalized to one, along a transect from coastal to offshore waters off the Falkland Islands, SW Atlantic during August 2020 to January 2022. Note: Sampling station (left) and time point (right) indicated by vertical lines.
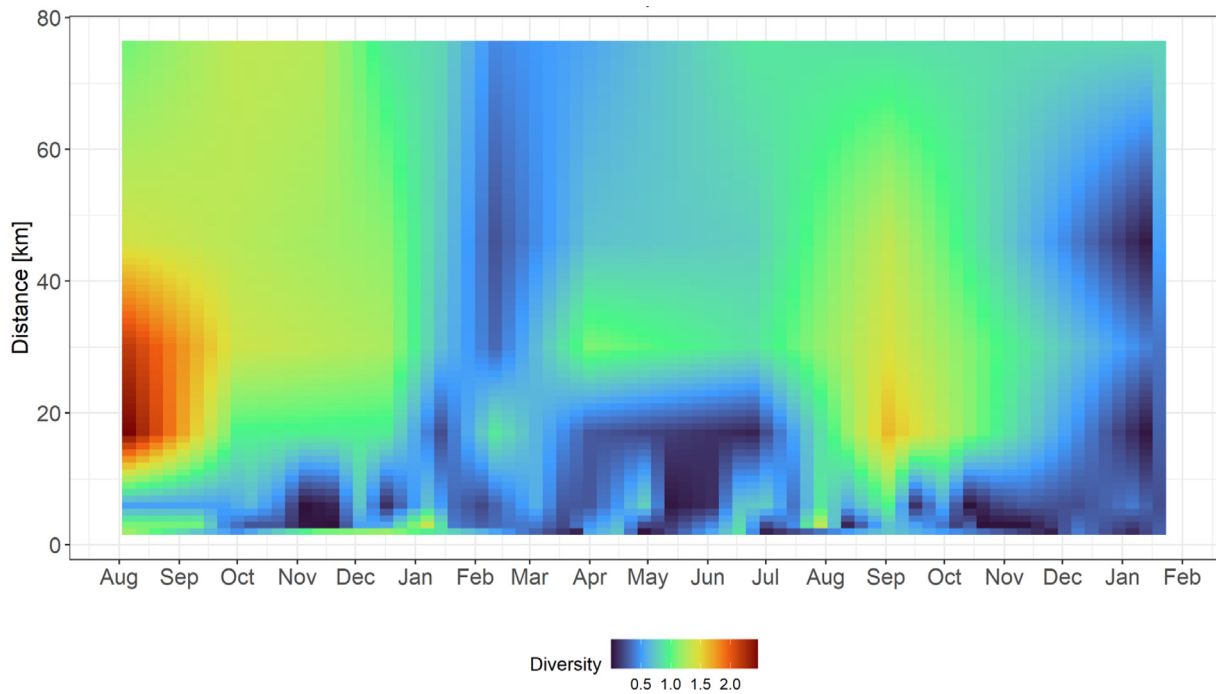

Fig. 4. Linear extrapolated mesozooplankton diversity indices (H') over 18 months (August 2020–January 2022) and distances ranging from 2 to 76 km from shore. Original data were extrapolated to increase resolution to one data point per week and one kilometre distance.

Sea surface salinity (SSS) varied between 33.8 and 34.1 (average = 33.9). Highest values were observed in September 2020 and February 2021. Spatially, SSS increased with distance from shore being the highest at P15.

Values for pH were ranging from 8 to 8.1. Values peaked during November and December of both years with a maximum value in November 2020. Within the narrow window observed,

overall higher values were found at shallower, nearshore stations (mean = 8.1 ± 0.04).

Testing the potential impact of environmental data on the plankton community with the GAM showed that distance (p < 0.001) and SST (p < 0.001) had a significant impact on the total mesozooplankton biomass. Biomass decreased with increasing distance from shore as well as with increasing SST (Fig. 3).
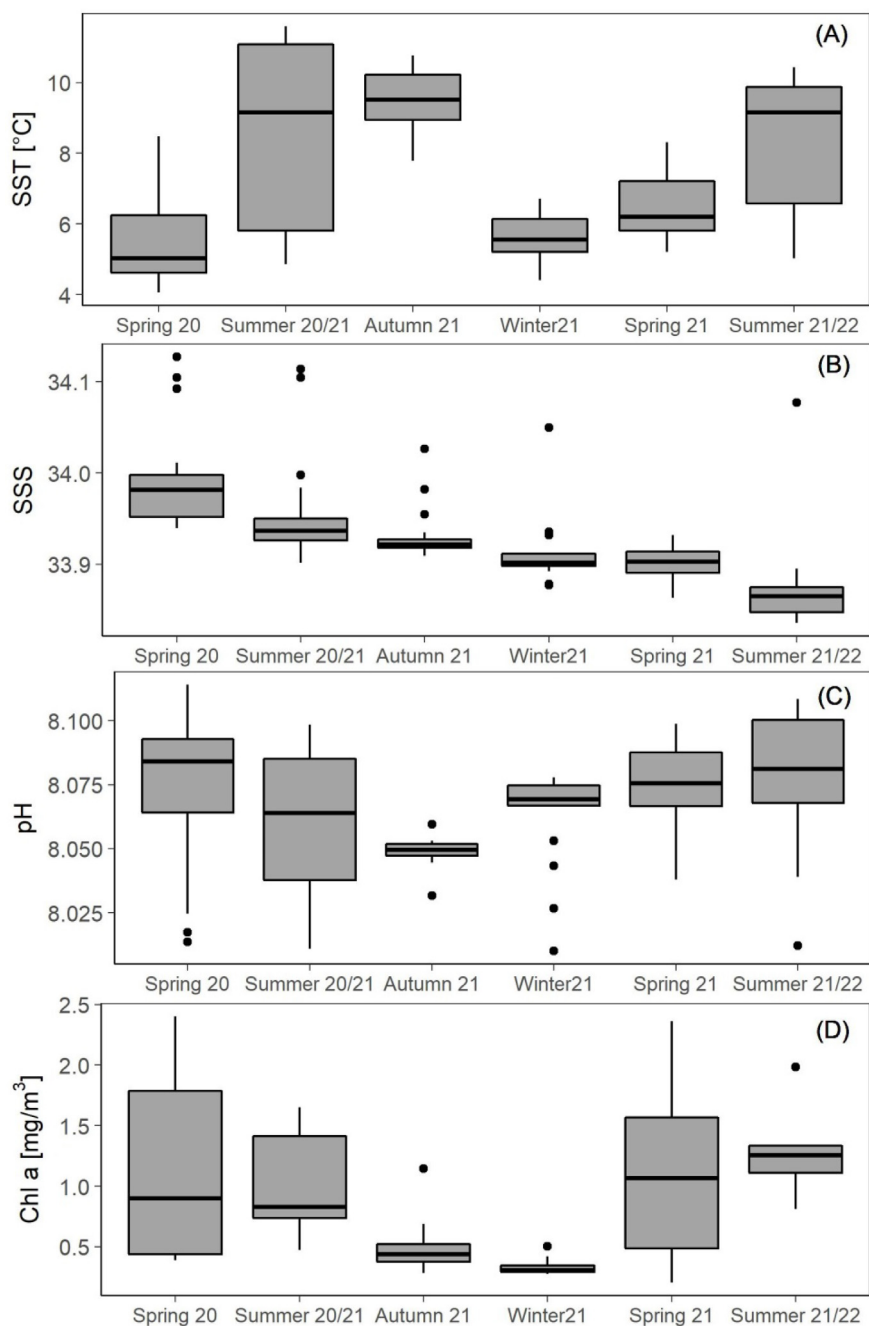
Fig. 5. Measurements of (A) SST [°C], (B) SSS, (C) pH and (D) Chl *a* [mg m^{-3}] for 6 investigation periods. Data summarized for 7 stations east of the Falkland Islands, SW Atlantic during September 2020 to January 2022.

Table 3
Effect of each explanatory variable and interaction on biomass in the performed GAM. df$_e$ = expected degrees of freedom, F value and *p*-value.

Biomass [g m^{-3}]	df$_e$	F-value	*p*-value
Distance [m]	1	15.775	<0.001
SST [°C]	3	10.453	<0.001
Chl *a* [mg m^{-3}]	1	2.764	0.098
SSS	1	0.051	0.821
Distance:SST	2.551	1.875	0.151
Distance:SSS	15.098	8.07	<0.001
SST:SSS	15.763	4.123	<0.001

Additionally, interactions of distance with SST and distance with SSS correlated with total mesozooplankton biomass significantly (Table 3; Fig. 6). The model explained 64.5% of the total variation.

The performed GAM indicated a significant correlation (p < 0.001) between pH and diversity (H'). Distance did not correlate with H'. However, the interactions of distance with SST, SST with chl *a*, distance with SSS, SST in summer and chl *a* in winter displayed significant interactions with diversity (Table 4; Fig. 7). The model explained 87.5% of the total variation.

4. Discussion

The present study provides the first investigation of the seasonal variability in zooplankton community composition and biomass near the Falkland Islands in the SW Atlantic Ocean, highlighting the dominance of copepods, *Grimothea gregaria*, and euphausiids, and revealing significant relationships between species abundance and SST, as well as distance from shore.
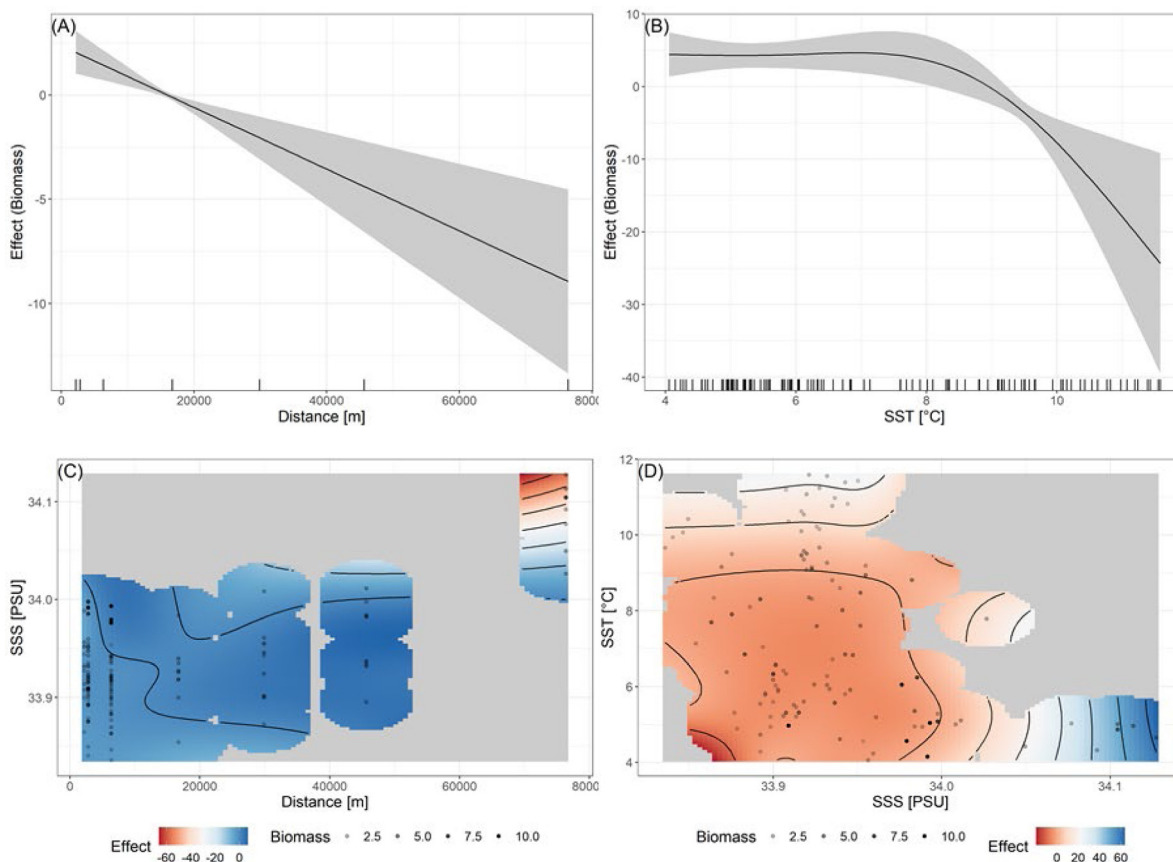
Fig. 6. Results of the GAM analyses for the effect of (A) distance, (B) SST, (C) interaction of distance and SSS and (D) interaction of SSS and SST on mesozooplankton biomass. SSS = sea surface salinity, SST = sea surface temperature. Grey areas indicate no observations in these combinations.

Table 4

Effect of each explanatory variable and interaction on diversity in the performed GAM with df_e = expected degrees of freedom, F-value and significance level (p-value).

Diversity	df_e	F-value	p-value
Distance [m]	1	0.279	0.598
SST [°C]	0.8	0.001	0.981
Chl a [mg m^{-3}]	0.8	0	0.993
SSS	1	7.899	0.006
pH	1.265	61.745	<0.001
Distance:SST	15.632	7.281	<0.001
SST:Chl a	13.299	4.957	<0.001
Distance:SSS	15.999	5.736	<0.001
Distance:pH	1.964	0.759	0.31
Season	–	0.385	0.764
SST:Winter	0.8	0.016	0.91
SST:Spring	0.8	1.053	0.36
SST:Summer	7.296	4.013	<0.001
SST:Autumn	0.8	0.512	0.523
Chl a:Winter	3.301	6.773	<0.001
Chl a:Spring	0.8	0.001	0.973
Chl a:Summer	5.294	2.425	0.024
Chl a:Autumn	3.408	0.574	0.584

We found that biomass decreased with distance from shore. Seasonal analysis revealed a yearly peak of mesozooplankton biomass and diversity index (H') in austral-spring and summer. Moreover, fluctuations of biomass and diversity were more pronounced nearshore than offshore, where biomass and diversity (H') of the mesozooplankton community are more stable throughout the seasons. Those differences are mainly related to the variation in SST, while pH had a significant correlation with mesozooplankton diversity, SSS and chl a had lower influence onto the community composition.

Copepods represent the most abundant group of marine metazoans worldwide (Humes, 1994). In the current study, the total number of copepods constituted about 86.6% of the total composition using a 350 μm mesh net (Table B.1). This is a comparable value with estimated density contributions of over 77% of copepods in the mesozooplankton community in the south western Atlantic ocean recorded by Thompson et al. (2013) using a smaller sized (20 μm) mesh net. However, the current study design with a coarser mesh net excluded zooplankton under 300 μm, not sampling a majority of small copepods (up to 80% of all copepods; Hopcroft et al., 2001; Cepeda et al., 2018; Garcia et al., 2021). Despite this cut-off, we still found a dominance of copepods, indicating that if we had used smaller net sizes, the dominance in numbers would have been stronger still. As many copepod species are present all year round, representatives of this group are often the first to increase in abundance in spring (Lindahl and Hernroth, 1983; Gabaldón et al., 2019; Almén and Tamelander, 2020). Increases in phytoplankton abundances due to increased light intensity in spring support blooms of herbivorous copepods in the south western Atlantic, which are preyed upon by carnivorous copepod and larger zooplankton species (Thompson et al., 2013). This reflected the measured biomass peaks of mesozooplankton in late autral-spring/early austral-summer prior to decreasing biomass off mesozooplankton towards austral-autumn and winter. Gabaldón et al. (2019) explained the general autumn drop of zooplankton biomass by (a) a lack of food items for herbivorous copepods after intense grazing and (b) increased predation pressure by higher trophic
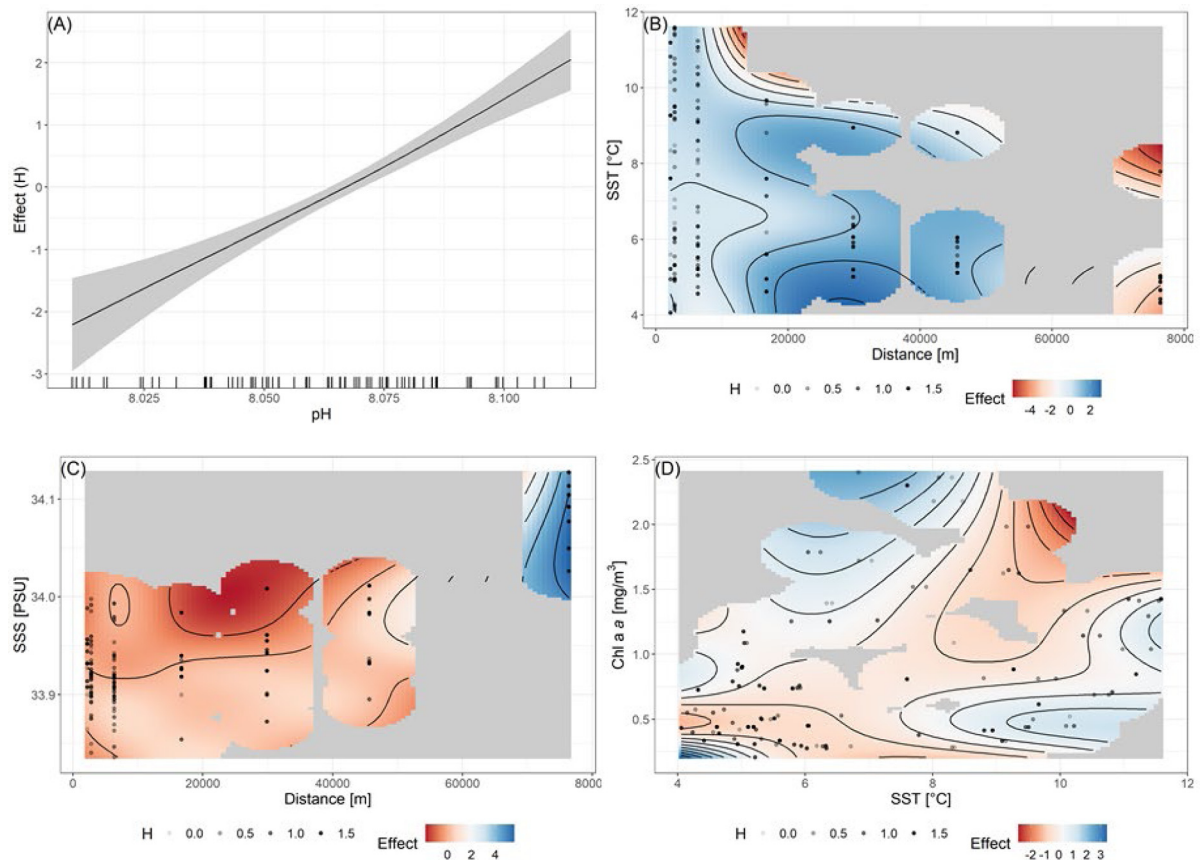
Fig. 7. Results of the GAM analyses for the effect of (A) distance, (B) SST, (C) interaction of distance and SSS and (D) interaction of SSS and SST on mesozooplankton diversity. SSS = sea surface salinity, SST = sea surface temperature. Grey areas indicate no observations in these combinations.

levels. Copepod species represent an important link in the pelagic carbon flux to higher trophic levels such as fish (Mauchline, 1998; Spinelli et al., 2016; Brennan et al., 2020). Further, *G. gregaria* contributed significantly to the mesozooplankton biomass close to shore (Fig. 2). Multiple larval stages of *G. gregaria* were present in the water column between August and late November during the sampling period. Castro et al. (2021) explained the predominance of early planktonic *G. gregaria* larvae in terms of biomass in the Beagel Channel by the lack of diel migration: prezoea and zoea larvae remained in the upper 100 m and therefore benefitted from higher phytoplankton concentrations and reduced food competition at night. High predation pressure by various fish and squid species (Vinuesa and Varisco, 2007; Büring et al., 2022) is potentially linked to the decrease in crustacean biomass in summer. Another confirmation of the existence of this trophic link was found when lower biomass of mesozooplankton species (e.g. *G. gregaria*) during the second sampling year were followed by seldom occurrence of fish larvae, even though we did not quantitatively capture those with our selection of sampling gear. Additionally, ontogenetically driven vertical migration towards benthic habitats, as shallow as 40 m depth in San Jorge Gulf, SW Atlantic (Vinuesa and Varisco, 2007), contributed to the complete absence of *G. gregaria* from samples from late austral-summer until early austral-winter.

For euphausiids no conclusive geographic distribution pattern could be identified which is probably explainable by the grouping of all euphausiids species together due to identification problems of juvenile and damaged individuals. However, in general, different strategies of seasonal migration seemed to have a big influence on mesozooplankton biomass. For instance, a contrasting migratory behaviour was observed for other species e.g. *T.*

macrura, where smaller individuals were found nearshore prior to increased abundances of larger individuals offshore. Similar migration patterns were identified for amphipods and fish larvae during this study. Shallow, nearshore habitat of the Falkland Islands seemed to provide a valuable nursery area for various mesoplanktonic species.

At offshore stations stable but low mesozooplankton biomass in spring/summer were followed by a blooming period between March and September 2021. Low biomass during spring could have been a result of increased predation upon pelagic and larger zooplankton specimen, e.g. Chaetognatha, mostly appearing offshore, as have similarly been documented for the Burdwood Bank, SW Atlantic (Spinelli et al., 2016). Additionally, mesozooplankton abundances are depth dependent (Vereshchaka et al., 2017). As samples could not be restricted to certain depths, no depth dependent accumulations of taxonomic groups were identified. By sampling the whole water column, abundances were integrated over depth and resulting biomass only represent a cumulative biomass over all depths up to 500 m. To account for this potential heterogeneity, more fine-scale methods would be necessary to resolve depth-specific distributions. Some groups i.e. ostracods inhabit deeper water layers beneath 200 m depths (Nogueira and Brandini, 2018). However, most species stay above 100 m depths for the majority of time (Hobbs et al., 2021). Overall, biomass at all stations were comparable to previous published measurements in the South Atlantic (Melo Júnior et al., 2016; Vereshchaka et al., 2017). The study design utilized a coarse mesh net and freezing of samples for preservation due to logistic limitations. We would like to point out that future studies may benefit from using a finer mesh size net and different preservation methods to better capture the gelatinous zooplankton community and

smaller metazooplankton members (Cepeda et al., 2018). In particular larvaceans, that are generally the second most abundant mesozooplankton group following copepods across ecosystems world-wide if appropriately sampled (Jaspers et al., 2023), are likely to be missed by our coarse meshed nets. It has been shown that >200 μm nets considerably under-sample the larvacean community (as reviewed in Jaspers et al., 2009). Therefore, regular sampling at all stations with a smaller mesh size, oblique tows over pre-defined depths and direct preservation in formalin could verify this.

As the Patagonian Shelf is located south of 48°S, a lower diversity compared to more tropical regions like south India was expected, where H' reaches over 3 (Thirunavukkarasu et al., 2020). The determined diversity indices in the present study were low (Fig. 4) even compared to Arctic values e.g. mean H' = 1.62, in Barents Sea 2006 (Dvoretsky and Dvoretsky, 2010). H' has to be handled with caution as species identification did not reach species level for all mesozooplankton items, especially copepods, which would lead to considerably higher H' if appropriately included. Nevertheless, our data inform about general temporal and spatial diversity trends across larger mesozooplankton groups. Higher diversity around 30 km from shore and a trend of increasing diversity with increasing distance from shore found in our study is supported by previous investigations (Nogueira and Brandini, 2018; Thirunavukkarasu et al., 2020). These studies found influx of nutrients as the main factor explaining temporal diversity variation in other regions like Brazilian estuaries and southern India (Nogueira and Brandini, 2018; Thirunavukkarasu et al., 2020). Even though we did not analyse nutrient concentrations directly, Chl a concentrations showed higher levels in spring and we can use this as a proxy indicating that similar mechanisms are at play in the Falkland Island, where the nutrient rich subantarctic water upwells along the shelf (Matano et al., 2010).

Next to nutrients, light and SST are considered as triggers for start and end of planktonic blooming seasons (Mackas et al., 2012; Giménez et al., 2018; Gabaldón et al., 2019). While daylight intensity was not considered in the current study, comparable impacts of temperature were determined. As most samples at offshore stations included the community from few meters above the seabed to the surface, hence above and below the thermocline, significance of temperature for biomass could be masked at deeper stations. However, in shallow, nearshore waters an increase of SST can be assumed to have initiated reproductive seasons (Miller et al., 1991). To improve explanatory power of temperature influence, a time offset could be taken into consideration as many reproductive mechanisms are characterized by a time-lagged response (Mackas et al., 2012). Nevertheless, high chl a values indicated high abundance of phytoplankton in the water column (Thompson et al., 2013). The mesozooplankton community is highly dependent on primary production as many copepod species feed upon its components (Aguirre et al., 2012; Gabaldón et al., 2019) and therefore chl a represents an important trigger for the mesozooplankton diversity of the SW Atlantic (Acha et al., 2018; Marrari et al., 2011; Aguirre et al., 2012; Thompson et al., 2013).

The mesozooplankton community presents an important link in the food web between phytoplankton and higher trophic levels in the region and different food web connections can be linked to considerable variations in production estimates of higher trophic level (i.e. fish). Due to the strong link between primary production and higher trophic levels, small seasonal changes of lower levels cascade through the food web (Cheung and Pitcher, 2005b) at even higher velocities compared to land based systems (Gabaldón et al., 2019). Büring et al. (2022) found mesozooplankton (predominantly euphausiids) as the main source of nutrition for early life stages of D. gahi in the Falkland Islands and the same applies to other commercial fish and squid species in the southern Patagonian LME (Laptikhovsky and Arkhipkin, 2003; Arkhipkin et al., 2003). Therefore, variation of mesozooplankton biomass (indicated by their developmental and reproductive cycle), have been shown to trigger migration, abundance and ontogenetic development of fish and squid in the Patagonian LME (Agnew, 2002; Mianzan and Cornelius, 1999; Omori and Hamner, 1982). In contrast, higher fishing efforts can reduce predation pressure on mesozooplankton, which could trigger changes in the mesozooplankton biomass. We highlight that future research should focus on the zooplankton community around the Falkland Islands in order to quantify interactions between mesozooplankton and higher trophic levels in this highly productive marine ecosystem.

5. Conclusion

In conclusion, this study highlights the importance of understanding the complexity of the mesozooplankton community in Falkland Island waters, as it provides the base of the food web of the ecosystem. The local plankton community is dominated by crustaceans i.e. copepods, next to Grimothea gregaria and euphausiids. A high mesozooplankton biomass in shallow, nearshore waters was observed. SST was the main impacting factor as initiator and driver of seasonal cycles of all components. Potential influence of predation within the planktonic community and from higher pelagic levels emphasized the importance of biotic interactions regulating community structure and the key role of mesozooplankton for the local food web. As the Falkland Island waters represent an important hatching and feeding ground for various species in key positions of the Patagonian LME ecosystem, research focussed on lower trophic levels in the area will improve ecosystem models and fisheries management in the SW Atlantic and support predictions of future ecosystem changes.

CRediT authorship contribution statement

Rebecca Piontek: Conceptualization, Methodology, Formal analysis, Writing – original draft, Visualization. **Cornelia Jaspers:** Writing – review & editing, Supervision. **Maarten Boersma:** Writing – review & editing, Supervision. **Alexander Arkhipkin:** Conceptualization, Writing – review & editing, Supervision, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary material related to this article can be found online at https://doi.org/10.1016/j.rsma.2023.103147.

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