Historical abundance and distributions of *Salpa thompsoni* hot spots in the Southern Ocean, with projections for further ocean warming

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Abstract

Over the last three decades, a significant variability in *Salpa thompsoni* occurrence has been observed in response to the ENSO fluctuations, changes in sea surface temperature and ice-cover extent. In this study, we analyzed historical data on *S. thompsoni* from the SW Atlantic Southern Ocean which spanned 20 years. This data series allowed to track previous fluctuations in Antarctic salp abundance and distribution, combined with different environmental conditions. The results revealed that Antarctic salps prefer deep, open, ice- free waters, which are characteristic of Circumpolar Deep Waters. Hot spot analyses confirmed that the highest number of *S. thompsoni* in the 1980's were located within the areas where sea ice was present. They were also recorded further south than 68°S in the presence of ice-cover and water temperature below 0°C. This may suggest that *S. thompsoni* is able to adapt to less suitable conditions and reproduce in cold, southern waters.

Prediction of future *S. thompsoni* distribution, with simultaneous water temperature increase, showed that the range of occurrence would move southwards by over 200 km in the coming 50 years.

Key Words: Hot spot analysis, projections of *Salpa thompsoni* future distribution, probit regression, Antarctic ecosystem functioning

Introduction

Over the last 30 years, the rise of atmospheric greenhouse gas has influenced the average global temperature, with an increase of 0.2°C, with the mean global sea surface temperature (SST) increasing by approximately 0.4°C since the 1950s [1,2]. Ocean heating is particularly pronounced in the most vulnerable areas which include the Southern Ocean, especially in the Antarctic Peninsula region [3, 4]. Even though, Turner et al. [5] suggested that there had been no evidence of climate warming in the mentioned area, based on the stacked air temperature records since the 1990s, there is still proof of sea ice decreasing in the Bellingshausen/Amundsen Seas, which can be tied to current ocean heating [6]. There is also confirmation of increasing frequency of extreme El Niño events, which have a great impact on Southern Ocean hydrology and water mass circulation [7]. In particular, summer water temperature along the Western Antarctic Peninsula increased by 1.3ºC over 50 years [8], and near South Georgia - a 1ºC increase has been recorded over the last 80 years [4]. The Weddell Deep Water (WDW) has warmed by ~0.032°C per decade, which was similar to the temperature changes around South Georgia and in the entire Antarctic Circumpolar Current (0.03–0.07°C per decade) [4, 8, 9]. The Antarctic Ocean is arguably the largest marine ecosystem on Earth and it is affected by a diverse array of environmental factors [10, 11]. Observed and projected environmental changes in Antarctic waters have been described by Gutt et al. [12] and this has revealed that large proportions of the Southern Ocean are and would continue to be affected by one or more climate change stressors.

The current phenomenon of environmental stress caused by climatic and anthropogenic pressures leads to shifts of frontal hydrological zones, existing habitats and is also likely to modify structure, spatial range and seasonal abundance of Antarctic key species [13-20]. The geographical range of crucial taxa can move southwards to remain in optimal thermal conditions, squeezing their distribution range closer to the Antarctic continent [16-20]. At the same time, more favorable habitats can be opened for more flexible organisms that are capable of adaptation like gelatinous salps [16, 19-24]. Antarctic salp *Salpa thompsoni*, together with the krill *Euphausia superba,* are among the most important filter-feeding species of the Southern Ocean, but only Antarctic krill constitute a major food source for many top predators, including fish, penguins, seals and baleen whales in a very short Antarctic trophic chain [18]. Salps are naturally present in the healthy ecosystem, fluctuating with oceanic modification [26, 26], and previous observations suggested that some predators even episodically include salps into their diet [27, 28]. Therefore, with an innate threat to krill abundance due to a changing climate, there is a growing concern that salps may locally replace krill as a food source. Salp dominated ecosystem would likely cause ripples up the Antarctic food chain as some predators will use salps as their food source better than others.

The most common Antarctic pelagic tunicate *Salpa thompsoni* [29] is typically oceanic and has a more extensive circumpolar distribution (45-55°S) [14,18,30], is not ice-dependent like *E. superba* and it is usually found in areas with lower food concentrations than those in which krill are found [14,16,20,21,30,31]. In most cases, an increase in the number of salps is observed simultaneously with a reduced presence of krill [16, 31, 32]. A full set of comprehensive studies on their abundance, range of distribution, changes in their life cycle and biology have already been performed [14,16,19,20,22,31]. Most of them confirmed that the greatest changes in salp abundance and distribution in the Atlantic Southern Ocean were associated with the sea ice loss, transitional periods between El Nino-La Nina (ENSO), and with the shifts of the Southern Boundary (SO) of Antarctic Circumpolar Current (ACC) [19, 20, 22]. Around the ACC, in the Antarctic Polar Front (APF) area, prevailing environmental conditions, such as low primary production, small food

particles [16, 18-20, 37], higher water temperature [35, 38] and low ice cover [16, 21, 39,] may drive massive salp blooms [39]. Evaluation of the *S. thompsoni* population may be problematic and underestimated due to a lack of clarity between surveys with regards to the identification of their life stages [22].

Mackey et al. [23] projected the southward shifts in the distributions of major Antarctic zooplankton taxa, however, without such a forecast for Antarctic salps. The comprehensive data about modification of salps/krill population were presented by Ross et al. [19]. They showed that krill abundance had decreased on the northern lines and had shifted 200 km to the south. If the trend of shrinking sea ice continues, within 2 decades, krill will disappear from the northern region of the Southern Ocean. Therefore, herein presented studies fortify foregoing knowledge by providing missing prediction of the salp population dynamics. The main aim of our research was to infer the historical abundance and distribution of *S. thompsoni* from the Atlantic Sector of the Southern Ocean from over twenty years of data collected (1975-2001) in order to discover how *S. thompsoni* handle less suitable environmental conditions and to determine what conditions promote the largest salp blooms. The purpose of the hot spot analysis was to detect the areas with the highest abundance of this species during the '70s and through to the 90's. The subsequent goal of this work was to predict the population and distribution of *S. thompsoni* with upcoming climate warming in the coming 50 years. In comparison to the previous studies, our data covers a wider time span and area, thus can provide an extension and supplement to existing information about the behavior of *S. thompsoni* population.

Materials and methods

Study area

The study area covered the region of the Western Antarctic Peninsula and South West (SW) Atlantic sector of the Southern Ocean (Fig 1).

Fig 1. The locations of the sampling stations.

The year of the cruise depicted in color.

The waters flowing around the Antarctic Peninsula are a specific and unique mixture of various water masses with different properties [40]. Here we can observe the mixing of warm, nutrient rich Circumpolar Deep Water (CDW) with cold, Antarctic shelves and coastal water masses, which have important effects on physical and biological processes in these regions [41]. Antarctic Peninsula (AP) water masses are well distinguished, due to bathymetric features such as continental slope, coastal or shelf regions [40]. This region is also more susceptible to the influence of the Antarctic Circumpolar Current (ACC) than other regions around the Antarctic where the ACC is distant from the shelf, typically separated by a polar gyre [40]. The marine ecosystems of the studied area are characterized by high diatom concentration and high primary production, krill predominance and a variety of higher vertebrate consumers [42]. Macronutrient concentration such as nitrate and phosphate are generally the highest in this area due to three factors: high concentrations in deep water, winter deep water mixing resupplying the surface layer after biological depletion, and micronutrient (iron) limitation [41].

Sampling

Salps were collected during the German and British research surveys (RV 'Walther Herwig', 'John Biscoe', 'Polarstern' and 'Meteor' cruises) using a Rectangular Midwater Trawl (RMT8) (mesh size 4,5 mm, mouth opening of 8m^2) [43] between 1975 and 2001, during early summer/late autumn. The RMT8 was equipped with a real-time depth recorder (TDR) and sampled from the upper 200 m of the water column or 10 m above the bottom, in shallow areas. A double oblique net tow was carried out routinely at all stations with a standard station grid. Calibrated flowmeters, mounted on the net frame, were used to estimate the volume of filtered water during each haul. Filtered water volume was calculated using equations from Pommeranz et al., [45], at a tow speed of 2.5 to 0.5 knots. All samples from the surveys were processed at sea. Immediately after the tow,

salps were removed and counted prior to other sample processing and were stored in 4% buffered formaldehyde for later measurements. Water temperature (T) and salinity (S) were measured prior to sampling (upper 200 m), however, this data was available only for a limited number of samples: T for 461 samples and S for 212 samples. Sea ice cover was estimated during all cruises, according to the scale 0-3, where 0 equaled no ice, and the remaining categories illustrate increasing ice cover density. Ice cover 3 equaled the largest degree of ice, but sampling was still possible.

Additional sea surface temperature and sea ice index data

Temperature and salinity were not measured during all sampling surveys, therefore we decided to expand our dataset using available HadISST1 product of Sea Surface Temperature (SST). Maps were published by the Met Office Hadley Centre for Climate Prediction and Research. Continuous SST maps had been created using the Reduced Space Optimal Interpolation (RSOI) technique. Original data from the Met Office Marine Data Bank (MDB) had been corrected for bias and gridded onto a 1° area grid. Whilst a consistent product, 1871-1995 included the monthly median SSTs from the Comprehensive Ocean-Atmosphere Data Set (COADS). Moreover, from January 1982, information from the satellite AVHRR sensor had been incorporated into the dataset, in order to significantly increase spatial data coverage and thus product quality [45].

The information about sea ice cover was obtained from the National Snow and Ice Data Center (NSIDC) for the time range of November 1978 up to the present. It was used to test the influence of sea ice abundance during the winter before a sampling campaign on the distribution and number of salps collected over the following summer months. The ice occurrence was mapped for the entire region south of 39.23° S and projected onto a plane in a Polar Stereographic Projection at 25 km spatial resolution [46].

Data analysis

Statistical analyses were conducted using STATISTICA 12.0 PL (Statsoft Inc.) and CANOCO 5 software. In order to test the presence/absence of salps in all samples, we tested sampling years as well as environmental variables for which we have the most complete datasets

with ice concentration and water depth, using Pearson's chi-squared tests and Levene's test, respectively. A multivariate probit regression model was used to evaluate the combination of factors for which the maximum likelihood of the appearance of salps was calculated. To find out which environmental variables significantly influenced the number of *S. thompsoni,* the following analyses were performed on the log transformed [x'=log (x+10)] abundance data (ind. m^{-3}). The analysis of variance (ANOVA) was used to test if the sea ice concentration (satellite dataset) in the preceding winter season has any impact on the number of salps during the closest following Antarctic summer. Additionally, a Generalized Additive Model (GAM, Poisson distribution) implemented in CANOCO 5 was used to examine the response of salps' abundance by determining their most probable spatial distribution in relation to sea surface temperature, bottom depth, and salinity.

Spatial analyses

The maps presenting spatial distribution and abundances of *S. thompsoni* were created using ESRI® ArcMap™ 10.5.1 software. The Global Moran's I statistic was used to test spatial autocorrelation of data (z-score: > 60, p-value: < 0.000) [47]. It revealed high clustering of data, so it was determined that the data set would be divided into three subsets based on the decadal time periods. Therefore, both ice cover interpolation and hot spot analysis were applied separately to each decade '70s, '80s, and '90s (including year 2001, because of its similarity to the cruises from 94/95 and 96/97). In order to interpolate ice coverage, the Kernel Interpolation with Barriers method was performed. The coastline of the Antarctic Peninsula from Antarctic Digital Database (ADD) was used as a barrier in the analysis. The kernel function was set to first order polynomial with the ridge parameter retaining the default value of 50.

The hot and cold spot analysis was conducted using the Hot Spot Analysis (Getis – Ord Gi*) tool. Point data were used in order to detect 'hot spot' areas with significantly high salp densities. This analysis computes a Z-score (a measure of standard deviation) for each point based on density value and neighboring spots (Z scores at the 95% confidence level are >1.96 for hot spots and < 1.96 for cold spots) statistically significant with $p < 0.05$.

In order to establish the future boundary of temperature optimum for the distribution range of salps, we used SST data from the Met Office Hadley Centre's [45]. Monthly SST maps were added to a mosaic using mean statistics for the years 1970 to 2001 (from December to March). The first boundary of salp distribution based on thermal conditions preference was created by extracting the periphery of 0°C temperature in the research area (temperature range for salp occurrence was based on our data analysis). The predicted boundary after a temperature increase of 1°C was extracted analogically from the periphery of 1°C. Since the sea surface temperature has increased by 1°C in the last 50 years, while maintaining a conservative approach, we have assumed that water temperature will increase by 1°C over the next 50 years.

Results

The extended collection resulted in 1872 samples, of which *S. thompsoni* was present in 1278. Our results from the long-term data series revealed significant annual variability in *S. thompsoni* abundance. Through the late 1970s and early 1980s mean abundances of *S. thompsoni* were relatively low in researched areas, with the exceptions of the cruises in 1975/76 and 1983/84. After season 1987/88, with very low salps densities (0.9 ind/1000m^3 ±1.26), the extremely high peak abundance occurred, with the mean density 1408 ind/1000m^3 (max. 25317.819 ind/1000m^3 ±2778.31). Although season 1994/95 was characterized by low salp abundances, their numbers began to increase rapidly and continuously over the following years (Fig 2).

Fig 2. Mean abundance of *Salpa thompsoni* sampled each year.

STD - standard deviation values above the line.

The probit regression models revealed critical environmental factors controlling the *S. thompsoni* occurrence (water depth, sea ice concentration, and water temperature).
Therefore, the maximum likelihood of S. *thompsoni* presence was computed based on the three maps considering the preferred conditions of this species: greater water depths – bathymetry map

[m], very low sea ice concentrations – sea ice concentration (interpolated from the dataset) and warmer water masses - sea surface temperature (Table 1).

Table 1. The model of the probit regression for the probability of *Salpa thompsoni* presence.

Environmental variable	**Bottom depth**	**Sea ice**	**SST**
Rating	0.00015	-0.39632	0.26181
Standard error	0.00006	0.16110	0.08335
t (445)	2.34494	-2.46010	3.14109
P value	0.01946	0.01426	0.00179

Satellite ice concentration data was used to reveal if the presence of ice a few months before the sampling season had an effect on the *S. thompsoni* occurrence in our samples. Interestingly, the probit model for the Sea Ice Index data (N=1311, $\chi 2$ =211.36, $p<0.0001$) confirmed that the sea ice concentration during the winter months (July and August) has a significant impact on the presence of salps in the following summer season. The high abundance of salps was also influenced by the sea ice concentration in the time of sampling (Kruskal-Wallis test H=33.98, $p<0.0001$).

The results of the multivariate probit regression model showed that the maximum probability of *S. thompsoni* occurrence was observed in areas with ice-cover degree between 0-1, and more often at the stations with greater water depth (Fig 3).

Fig 3. Multivariate probit regression model.

Probability of salps appearance under varying conditions of sea ice and bottom depth. The minimum likelihood marked in in dark green (>0.5), the maximum likelihood marked in dark red (>0.9).

However, further analysis confirmed that salps also appeared in less favorable ice conditions with ice-cover around 2-3 degree (Fig 4).

Fig 4. The abundance of *Salpa thompsoni* at stations with different sea ice classes. Determined median, percentile 25 and 75%, and the minimum and maximum values.

Generalized Additive Models (GAM) fitted for sea surface temperature (F=5.3, p=0.0054) revealed a uni-modal response, with the peak around 1°C (Fig 5), but numbers of *S. thompsoni* were also registered in the water layers with temperatures even below 0°C. GAM against salinity (F=5.8, p=0.0039) and bottom depth (F= 15.0, p<0.00001) did not give such a clear response. The highest numbers of salps seemed to be observed within waters with a salinity around 34-34.5. The same model used for the bottom depth showed the presence of three different peaks, indicating preference for shallow shelf waters with bottom depth around 300m, but also deeper open-ocean waters around 2000 -5000m bottom depth (Fig. 5).

Fig 5. GAM for the number of salps against

A) sea surface temperature, B) salinity, and C) bottom depth.

Hot Spot Analysis

Despite the fact that sampling sites in the 1970's were spread along the West Antarctic Peninsula region, near the South Shetland Islands, around South Orkney Islands in the Atlantic sector of the Southern Ocean., statistically significant hot spots were located mostly near Elephant Island, where ice concentration was degree 0 (Z-score > 1.67 and p value < 0.05). In the 1980's hot spot locations moved further to the south, but it could be related to wider sampling area. Regardless of the similarity between sampling coverages of WAP area, hot spots (Z-score > 1.7 and p value <

0.05) were placed in regions of the Biscoe Islands as well as Anvers Island and through the Bransfield Strait (Fig 6).

Fig 6. Hot spots of *Salpa thompsoni* distribution in decadal time series.

A) '70s; B) '80s and C) '90s. In the background - the interpolated ice concentration for the respective time series. Cold spot marked: in grey - 90% confidence, blue - 95% confidence, dark blue - 99 % confidence. Hot spot marked: in orange - 90% confidence, dark orange - 95% confidence, red – 99% confidence. Different sea ice degrees marked in: violet – without sea ice, dark blue- 1, sky blue- 2, light blue- 3.

Significant high densities of salps, assuming 99% confidence, were still found in the vicinity of Elephant Island like in the previous decade. The stations with high abundance of salps were in the areas with ice coverage classified as 1. Sampling stations in seasons 1994/95, 1996/97 and 2001 were all clustered around the Elephant Island region. This region showed *S. thompsoni* hot spots, with a high Z-score (up to 7.89) and p value <0.05.

Discussion

Our results revealed significant annual variability, presumably due to differences in environmental conditions prevailing during and before sampling years. In our study, we found four visible peaks with higher *S. thompsoni* numbers between years 1975/76, 1983/84, 1989/1990, and another salp increase from 1998 to 2001 (Fig 2). According to the previous studies [48], sea ice extent was decreasing from 1981 to 1984 when it reached the minimum extent, and our results revealed the peak number of salps in the next 1985 summer season. We noted the second salp peak in the 1990s (Fig 2), which also appeared after a prolonged period of decreased sea ice extent - from 1987 (high sea ice extent) until 1990 in South Georgia, Elephant Island, West Bransfield Strait, and North King George Island regions [24,48]. Other high peaks of salp abundance were noted in 1985, after 1982-83 El Niño periods, and in 1990, after the El Niño events in 1987-88 [48].

According to Loeb and Santora [18], the period 1999–2009 was characterized by increased influence of La Niña events and this had an impact on ocean and sea ice conditions [40, 49]. This is another confirmation that the southward expansion of salps is strongly connected to the observed decrease in sea ice cover within cold Antarctic Waters, and secondly, to the environmental modification which was related to previous ENSO periods [50]. All of these facts indicate, that the greatest peaks of salp densities are the most possible presumably after 3-4 years of low sea ice extent, and inter-annual variability in the salp number are correlated with El Niño Southern Oscillation indices (SOI and El Nino) prevailing over the previous 2 years [18]. The data reported the crucial months for salps, before the summer time and their breeding period, are July and August. Lack of sea ice in these months allows salps to form more vast and condensed aggregations during the following summer time.

Our results initially confirmed that the most important factor for *S. thompsoni* occurrence was sea ice concentration. Also, the previous studies revealed that salps were most frequently present in the ice-free regions [16, 19, 20, 22-24]. Although, further modelling showed that S. *thompsoni* may be present even with less suitable ice conditions, 2-3 ice degree, which means that they are able to exist in this environment. We estimated that the highest possibility for *S. thompsoni* occurrence is around waters with a temperature of 1-2°C, salinity of 34 (Fig 5), and expected more in deep sea areas, characteristic for the open ocean rather than the shallow waters. However, our GAM model rejected this theory and revealed that the highest salp number from October to March was located in the shallow shelf waters (predominately 300-600m deep) as well as within waters with greater depths of 2000-5000m. This could be partially explained by the characteristics of the ACC water masses and salps habitat preference within the area free of ice. The ACC pumps warm (>1.5°C), salty (34.65–34.7), and nutrient-rich Circumpolar Deep Water (CDW) onto the continental shelf below 200m [51], and moves salps towards the Antarctic continent and the surrounding islands to the Brasfield Strait areas [52], where they can be found in high abundance. According to the literature, higher abundance of *S. thompsoni* aggregates occur mostly

in the upper water column (200m) from November to March through chain release[18]. However, oozooids need to dive into deeper waters (300–1000 m depths). During salp blooms, their abundance is not only registered at the surface but also at greater depths.

The Hot Spot and Further Projection Analysis

The dataset was divided into three decadal time periods, ‘70s, ‘80s, and ‘90s which confirm that the *S. thompsoni* hot spot distribution, within the studied area, has been located mostly around Elephant Island. In the ‘70s and ‘90s their greatest numbers were observed mostly within open ocean, however, in the ‘80s *S. thompsoni* hot spots were located evenly within Islands around Brensfield and Gerlache Straits, as well as far south near the cold Bellingshausen Sea, where sea ice was present and water temperature was lower. This hot spot analysis has not indicated distribution changes but it may be related to a wider sampling site, which could be evidence of the existence of salps within the higher southern latitudes. The greatest salp number was recorded between 65-70°S in the presence of ice-cover and water temperature below 0°C, which may suggest that *S. thompsoni* is able to adapt to less suitable conditions in colder, shelf waters. The presence of *S. thompsoni* in areas further south can be explained by eddies and poleward intrusions of warm CDW (Circumpolar Deep Water) at depth, derived from the ACC [14]. The shelf waters of the Antarctic Islands are strongly affected by local heating, freshwater runoff and flow of warm waters from the AAC through the deep straits between Smith, Low, and Brabant Islands. CDW is present at depths ranging from 200 to 1000m and mixes with cold surface water masses from the Weddell and Bellingshausen Seas [52, 53]. With the ACC southward migration, seeds of salps could travel with these currents to the southern Polar Regions, causing a change in their distribution patterns and forcing salps to adapt to less suitable conditions. This would allow them to exist within the cold Bellingshausen Sea water masses. S. *thompsoni* generally occurs in warm water masses > 0 °C, between 45-55°S [30], but this study confirmed that a high number of mature individuals were observed south of the Southern Boundary (SB), demonstrating that *S. thompsoni* is able to undergo a complete life cycle in this area. Our results, together with the study presented by Ono et al. [54],

has revealed that *S. thompsoni* appeared across the SB of the Antarctic Circumpolar Current, and suggests that it is not a barrier preserving Antarctic waters from *S. thompsoni* invasion. Likewise, our results point out that salps are able to survive in areas with non-preferred environmental conditions (sea ice presence, decrease of temperature), which may indicate that they are also able to continue the reproduction process. A number of genetic studies further proved [55-57] that salps are highly flexible, capable of adaptation to the changing environmental conditions within different parts of the Southern Ocean. In contrary, the recent study of Goodall-Copestake [58] revealed that *S. thompsoni* reflects some genetic adaptations to high Antarctic conditions, but simultaneously shows that *S. thompsoni* appears to have been suffering in cold waters and so it may not be as fully adapted to the cold as previously thought.

Accordingly to the work of Mackey et al. [23] and Ross et al. [19], herein presented results expands foregoing knowledge about the dynamics of Antarctic salp populations and demonstrates predictions of their future distribution. In our study, we have made the inference about future salp distribution modification with the assumption that the water temperature will increase by 1°C, and results showed that the *S. thompsoni* range could move southwards by an average of 200 km. Results from data analysis indicate that high densities of salps were usually present in the areas of water temperature around 1-2°C and the border for their favorable reproduction is 0°C. The distribution of water masses warmer than 0°C overlapped with the areas of hot spots (WAP region). Taking into account climate fluctuations and temperature trends, we tracked the movement of the temperature boundary for salps for a hypothetical situation of ocean warming by 1°C for the next 50 years. The comparison of the locations of isotherms 0°C and 1°C revealed that massive blooms of *S. thompsoni* may shift their distribution southward into the Weddell Sea and closer to the Antarctic continent. Such temperature rise would enlarge their habitat area by nearly 530 000 km^2, which may exclude Antarctic krill and change the current Antarctic ecosystem completely (Fig 7).

Fig 7. Boundary of salp temperature optimum.

In the studied year (marked in light gray) and prognosis on its change after 1°C temperature rise (marked in dark gray).

Conclusions

Our study has confirmed that significant variability in *S. thompsoni* abundance is strongly connected to the observed sea ice cover decrease, and the environmental modification related to ENSO periods. Our work, together with the results of other authors, also marked strongly that the greatest peaks of salps are most likely after 3-4 years of low sea ice extent, and the El Niño Southern Oscillation indices prevailing over the previous 2-3 years. Herein, presented data shows that the crucial months for salps are July and August when the lack of sea ice allows salps to form more vast and condensed aggregations during the following summer period. Due to the increasing water temperature, reduction in ice cover and more frequent ENSO periods, after 1987/88 we may observe more rapid and immense salp bloom phenomena even within the high latitudes of the Southern Ocean.

Presented data revealed that Antarctic salps preferred deep, open, ice-free waters with temperatures around 1-2°C, which is characteristic of the Circumpolar Deep Waters. However, our results point out that salps are able to survive in areas with non-preferred environmental conditions (sea ice presence, lower water temperature <0°C), which may indicate that they are also able to continue the reproduction process.

Our results suggest that the SB of the ACC is not a barrier for *S. thompsoni* occurrence, because salps may exist in harsh conditions including the presence of ice. Our models revealed that the highest salp abundance was located at the shallow, cold shelf waters close to the Antarctic Peninsula. In the studied area, *S. thompsoni* hot spot distributions were dependent on the sampling location in a given period, and have been located mostly around Elephant Island. However, in the '80*s S. thompsoni* hot spots were located evenly within Islands around Brensfield and Gerlache Straits, as well as to the south near the cold Bellingshausen Sea. The greatest salp density was

recorded between 65-70°S in the presence of ice-cover and water temperature below 0°C. Salp occurrence could be partially explained by the characteristics of the ACC water masses and salp habitat preference within the area free of ice. Our work, together with studies on salp genome flexibility suggest that *S. thompsoni* may be able to adapt to less suitable conditions and even reproduce in colder, shelf waters.

The inference of future salp distribution demonstrated that the range of *S. thompsoni* would move southwards, enlarging their habitat area by over 500 000 km^2. Considering salp adaptation ability, this barrier may move even further to the south, and this kind of Antarctic zooplankton modification may lead to jelly-like zooplankton taxa domination in the Antarctic food-web. Summarizing, it is clear that salps are remarkably flexible and further studies are required to look at these unique animals more closely. It is important to continue studies about salps population dynamics and reproduction efficiency, but most importantly, expand the research on their adaptive capacity and response at the molecular level.

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Data archiving

This data was collected as part of a long-term project to provide and compile data on a range of krill and salp variables. Our data is available and deposited in the KRILLBASE DENSITY DATABASE.

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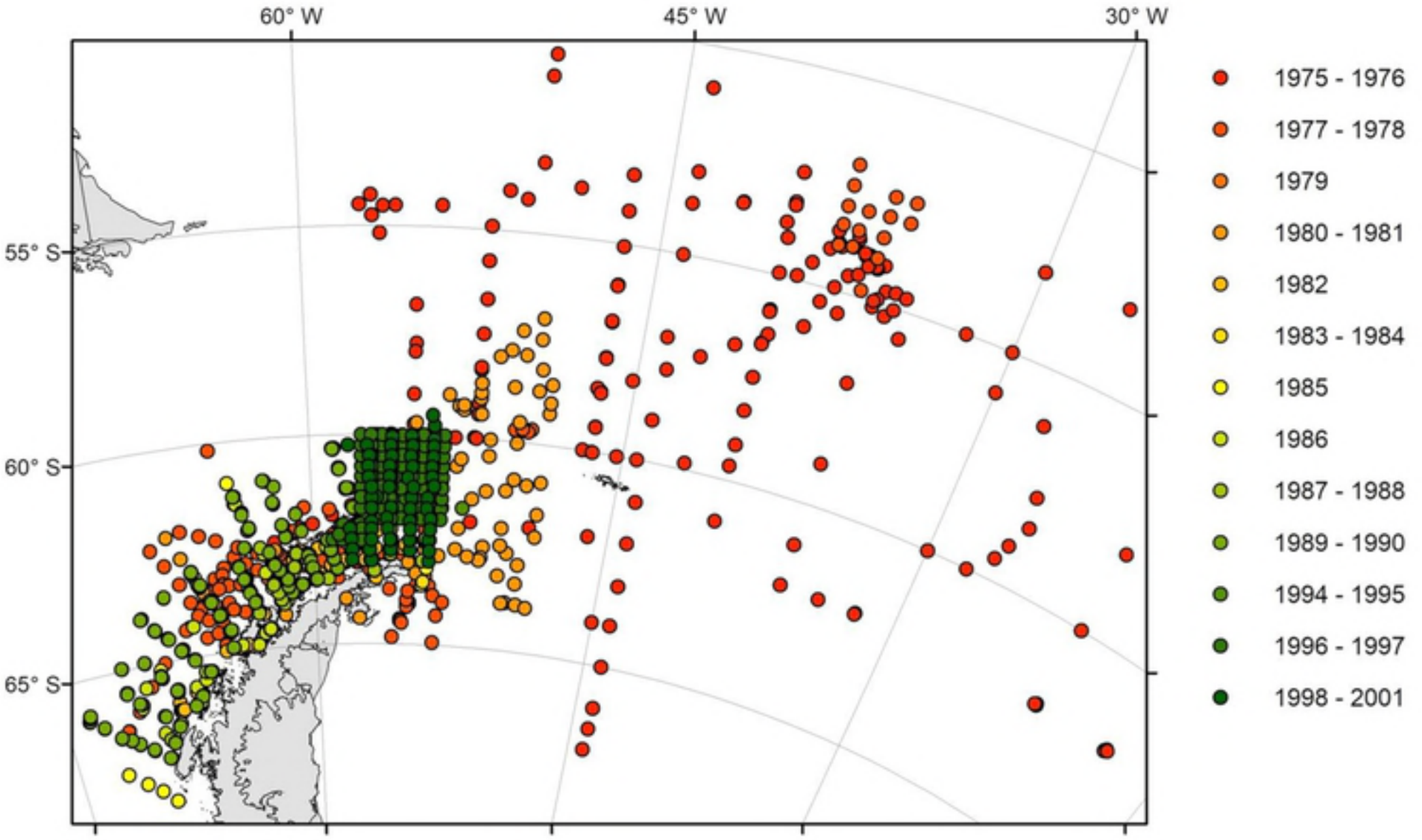
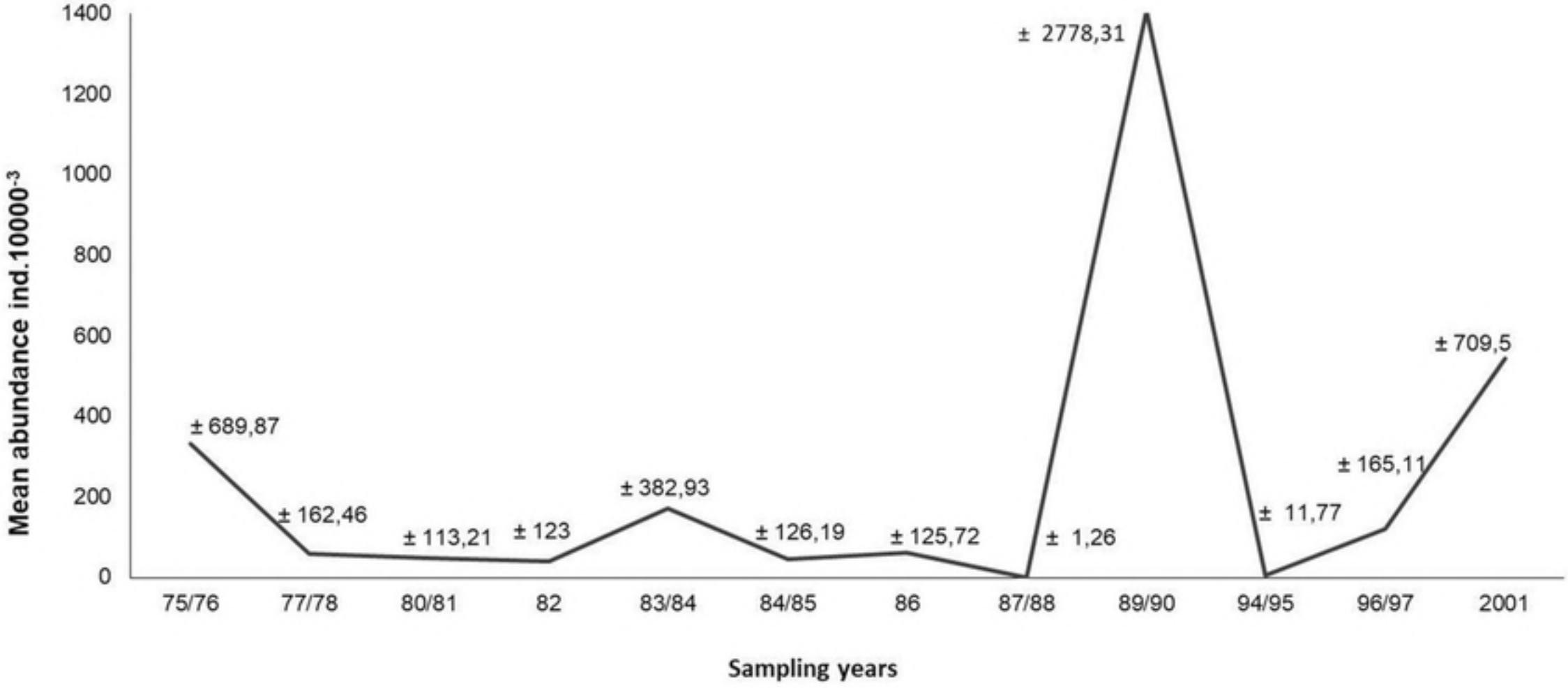
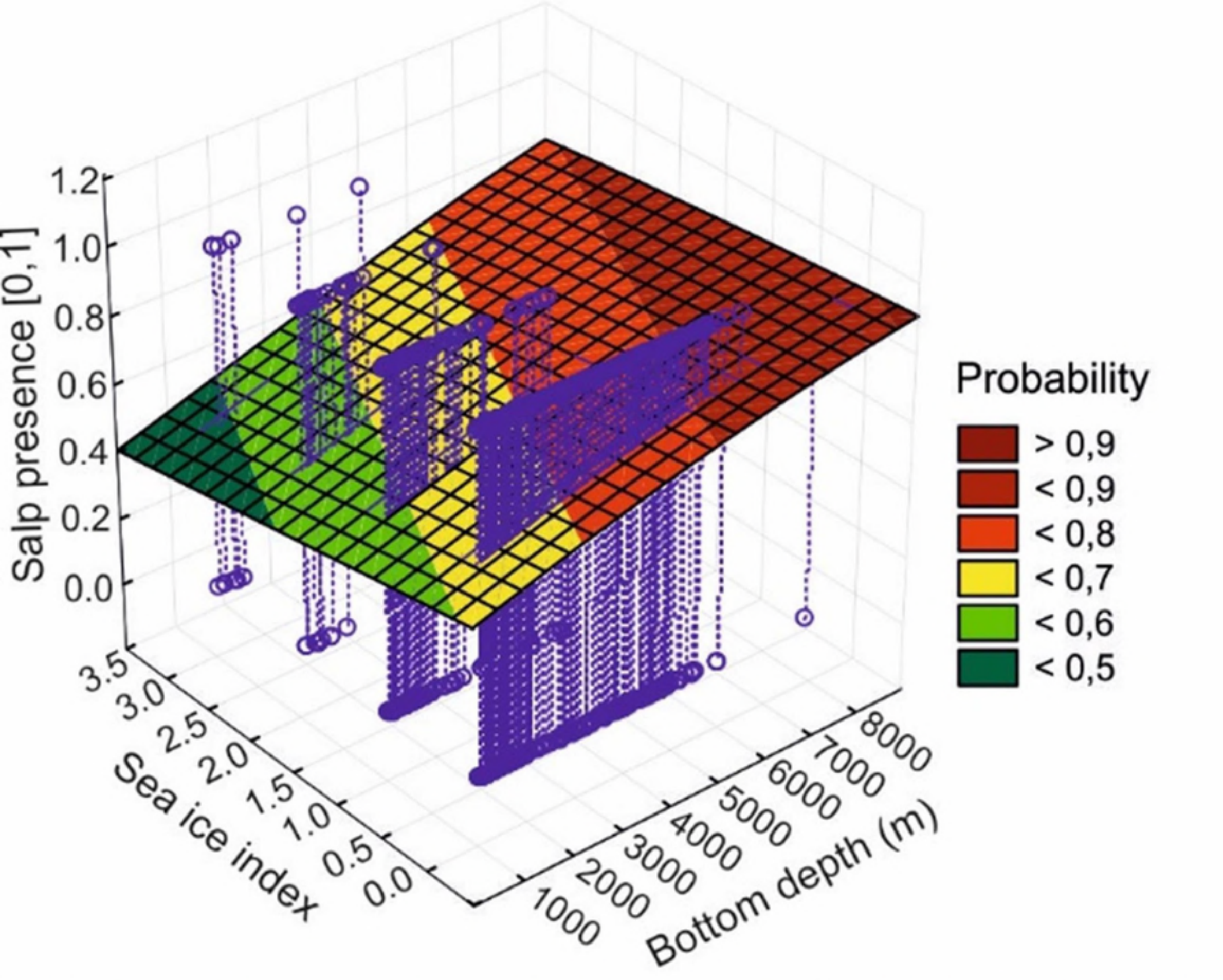

60° W
45° W
30° W
55° S
60° S
65° S
1975 - 1976
1977 - 1978
1979
1980 - 1981
1982
1983 - 1984
1985
1986
1987 - 1988
1989 - 1990
1994 - 1995
1996 - 1997
1998 - 2001

Figure

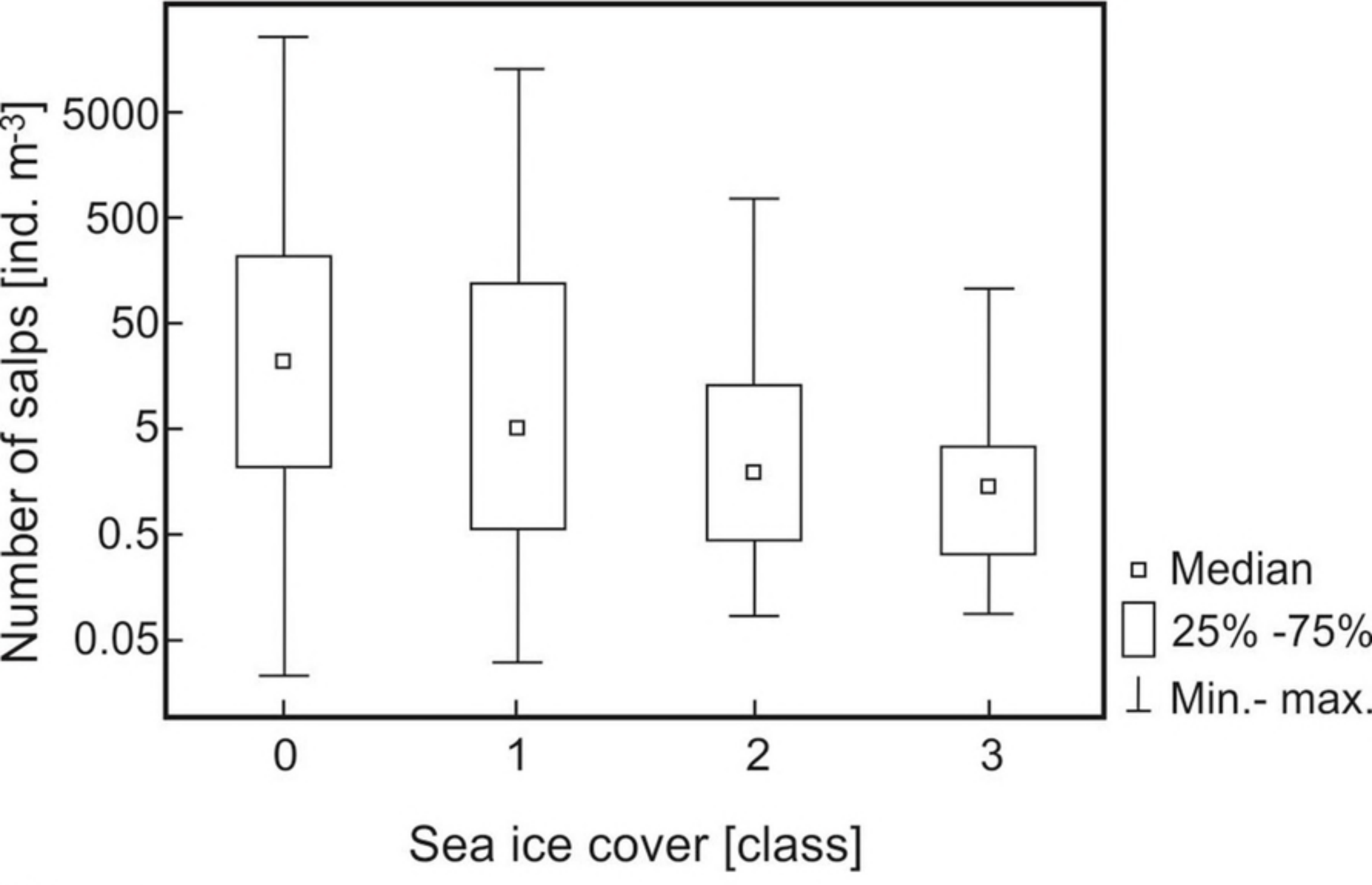

1400
1200
1000
800
600
400
200
0
Mean abundance ind.10000-3
± 689,87
± 162,46
± 113,21
± 123
± 382,93
± 126,19
± 125,72
± 1,26
± 2778,31
± 11,77
± 165,11
± 709,5
75/76
77/78
80/81
82
83/84
84/85
86
87/88
89/90
94/95
96/97
2001
Sampling years

Figure

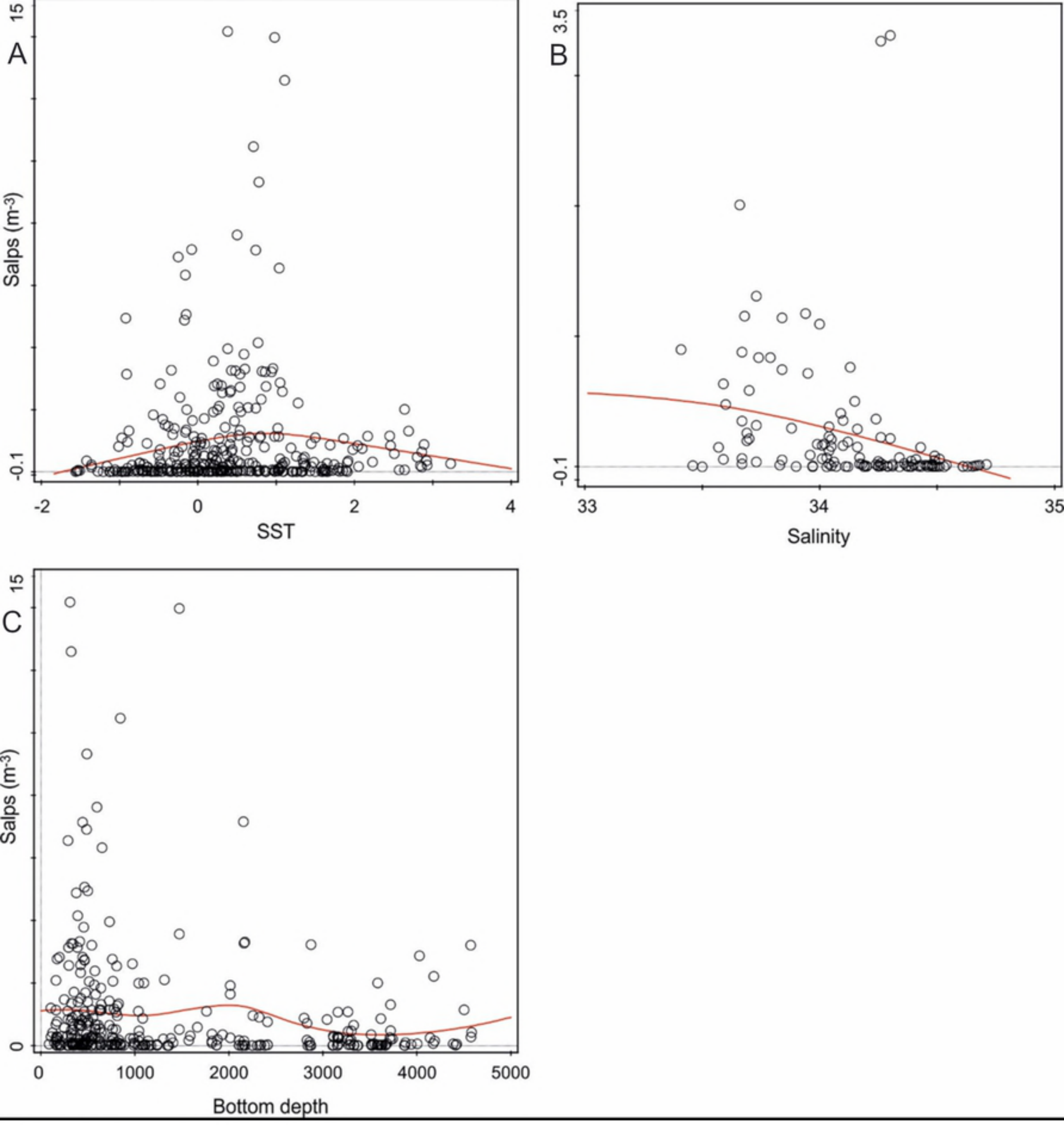


z=inormal(.32671011709901+(.11804701147E-3)*x+(-.1273533598162)*y;0;1)

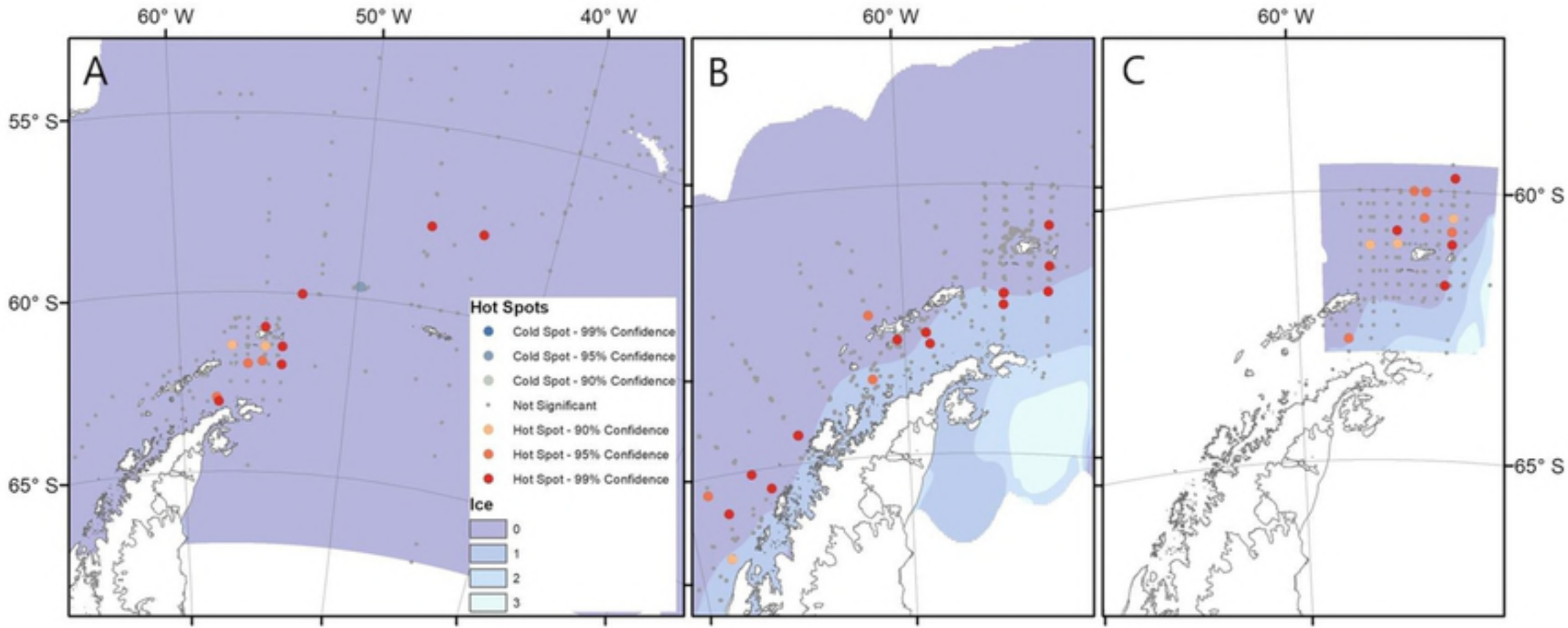
Figure


Number of salps [ind. m-3]
5000
500
50
5
0.5
0.05
0
1
2
3
Sea ice cover [class]
Median
25% -75%
Min.- max.

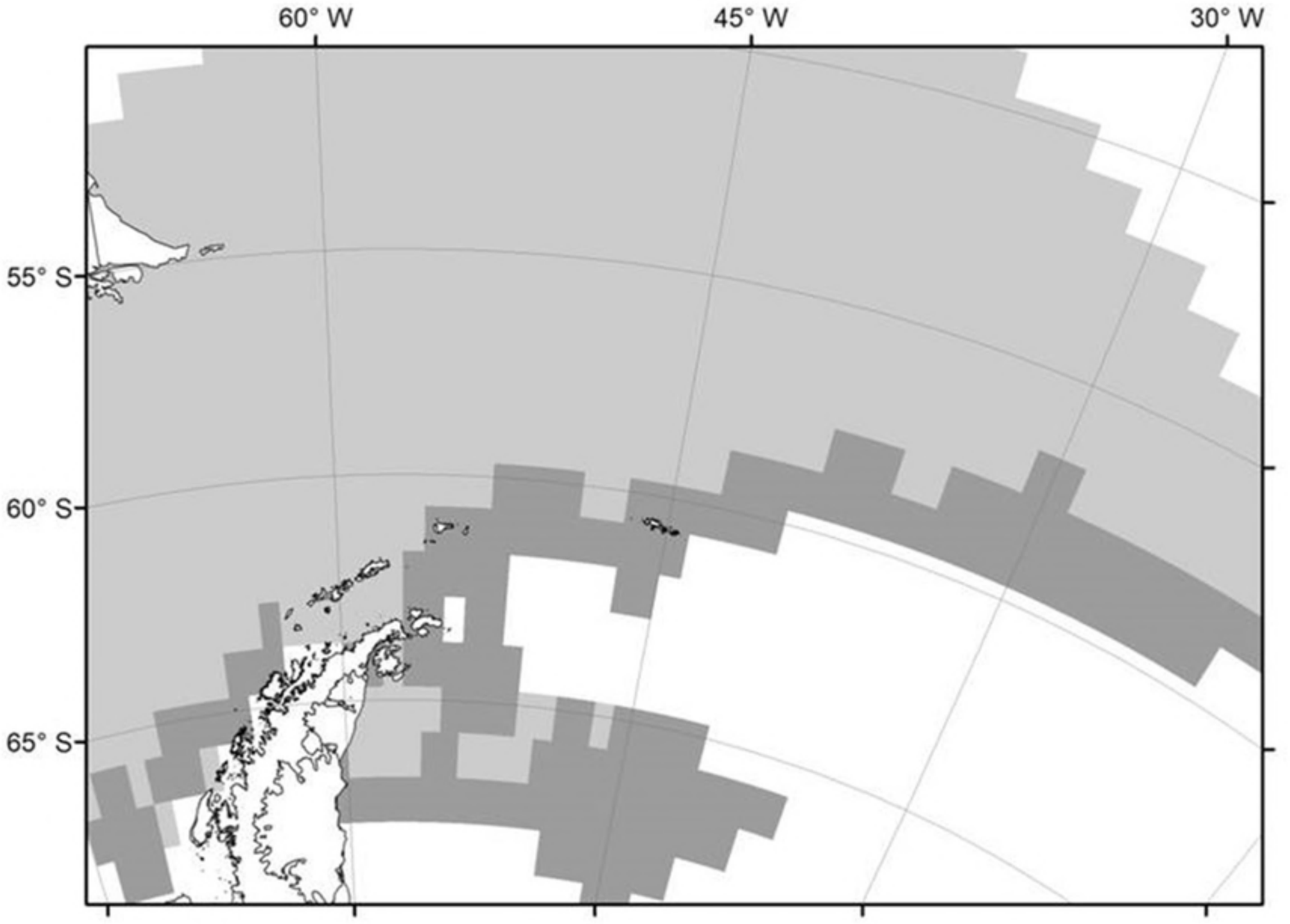
Figure


A
15
-0.1
Salps (m-3)
-2
0
2
4
SST
B
3.5
-0.1
33
34
35
Salinity
C
15
0
Salps (m-3)
0
1000
2000
3000
4000
5000
Bottom depth

Figure


60° W
50° W
40° W
60° W
60° W
A
B
C
55° S
60° S
65° S
60° S
65° S
Hot Spots
Cold Spot - 99% Confidence
Cold Spot - 95% Confidence
Cold Spot - 90% Confidence
Not Significant
Hot Spot - 90% Confidence
Hot Spot - 95% Confidence
Hot Spot - 99% Confidence
Ice
0
1
2
3

Figure



Figure