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

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Abstract

1. In contrast to Antarctic krill *Euphausia superba*, Antarctic salps (*Salpa thompsoni*) respond positively to warmer water temperatures and have the ability to create massive blooms under favourable conditions. Therefore, they can compete with krill for primary production. Over the last three decades, significant variability in *S. thompsoni* occurrence has been observed as a response to the environmental fluctuations of the Southern Ocean ecosystem (e.g. changes in sea surface temperature and ice-cover shrinkage around the cold Antarctic waters).
2. This study presents historical abundance data of salps from the south-west Atlantic Sector of the Southern Ocean, covering a time span of 26 years. These data allow tracking of fluctuations in Antarctic salp abundance and their distribution with bottom depth, temperature, and ice conditions, aiming to reveal salp hot spots and to predict the future range of *S. thompsoni* distribution with upcoming climate warming in the next 50 years.
3. Results showed the highest salp density in shallow shelf waters with ice cover and low temperatures between 1 and −1°C. In the studied area, *S. thompsoni* hot spots were located mostly around Elephant Island, but also the islands around Brensfield and Gerlache Straits, as well as to the south near the Bellingshausen Sea. Inferences made of future salp distribution suggest that the range of *S. thompsoni* will move southwards, enlarging their habitat area by nearly 500,000 km^2, which may have significant implications on the whole Antarctic food web. The information presented herein may be used for Antarctic ecosystem management, protection, and conservation.

KEYWORDS
Antarctic ecosystem, climate change, hot spots, long-term fluctuations, *Salpa thompsoni* distribution and abundance

1 | INTRODUCTION

Over the last 30 years, increasing atmospheric greenhouse gas has influenced the average global surface temperature to increase 0.87°C between 2006 and 2015 relative to 1850–1900 (Levitus, Antonov & Boyer, 2005; IPPC, Masson-Delmotte et al., 2018). Rapid heating is particularly pronounced in the polar regions, including the Antarctic environment (Zwally et al., 2000; Whitehouse et al., 2008). However, based on the stacked air temperature record since the 1990s, Turner et al. (2016) suggested that there was no evidence of climate warming in this area. Contrastingly, clear proof of decreasing sea ice extent has been recorded in the Bellingshausen and Amundsen Seas (Turner et al., 2016). In particular, summer water temperature along the Western Antarctic Peninsula (WAP) has increased by 1.3°C over 50 years (Meredith & King, 2005), and a 1°C increase has been recorded over the last 80 years near South Georgia (Whitehouse et al., 2008). Weddell Deep Water has warmed by ~0.032°C per decade, which is similar to the temperature changes around South Georgia and in the entire Antarctic Circumpolar Current (ACC) (0.03–0.07°C per decade) (Nicol et al., 2007; Whitehouse et al., 2008).

Environmental stress caused by climatic and anthropogenic pressures leads to shifts of frontal hydrological zones and existing habitats, and is likely to modify the structure, spatial range, and seasonal abundance of Antarctic key species (Froneman, & Perissinotto, 2002; Atkinson et al., 2004; Richardson, 2008; Loeb & Santora, 2012; Ross et al., 2014; Steinberg et al., 2015). Antarctic salp *Salpa thompsoni* (Foxton, 1961), together with krill *Euphausia superba* (Dana, 1850), are among the most important filter-feeding species of the Southern Ocean, but only Antarctic krill is considered a major food source for many top predators, including fish, penguins, seals, and baleen whales (Loeb & Santora, 2012). For example, the geographic range of *E. superba* can move southwards to remain in optimal thermal conditions, squeezing their distribution range closer to the Antarctic continent (Atkinson et al., 2004; Richardson, 2008; Loeb & Santora, 2012; Ross et al., 2014). Meanwhile, more favourable habitats can become available for organisms that are capable of adaptation, such as gelatinous salps (Mackey et al., 2011; Ross et al., 2014; Steinberg et al., 2015; Goodall-Copestake, 2016; Jue et al., 2016).

Therefore, owing to the current threat to already-decreasing krill numbers and changing climate conditions, there is a growing concern that salps may locally replace krill (Atkinson et al., 2004; Ross et al., 2014; Steinberg et al., 2015). Possible mechanisms underlying these observations include the southerly movement of the sea ice edge, water temperature fluctuations, reconstruction of phytoplankton structure, and changes in ACC transport pathways. All these factors might cause shifts in Antarctic krill populations and create a free ecological niche available for pelagic tunicates.

S. thompsoni is typically oceanic, with an extensive circumpolar distribution (45° – 55°S) (Foxton, 1966; Pakhomov, Froneman & Perissinotto, 2002). This species is not ice-dependent like *E. superba*, and it is usually found in areas with lower food concentrations (Siegel & Loeb, 1995; Loeb et al., 1997; Pakhomov, Froneman & Perissinotto, 2002; Atkinson et al., 2004; Steinberg et al., 2015). Antarctic salps prefer water masses of higher temperature (3–5°C) (Henschke & Pakhomov, 2018) across the Circumpolar Current. Therefore, the highest salp abundance is observed along with the absence, or at least really low numbers, of Antarctic krill (Siegel & Loeb, 1995; Atkinson et al., 2004). Previous studies have provided some evidence that the greatest changes in salp abundance and distribution in the Atlantic Southern Ocean are associated with sea ice loss, transitional periods between El Niño-La Niña, and shifts of the Southern Boundary (SB) of ACC (Siegel & Loeb, 1995; Chiba et al., 1999; Pakhomov, Froneman & Perissinotto, 2002; Atkinson et al., 2004).

The primary focus of this study was to identify the main barriers hindering salp occurrence and provide predictions of their future distribution. Based on historical *S. thompsoni* abundance data in the Atlantic Sector of the Southern Ocean, a spatial distribution of salp populations was reconstructed from the period 1975–2001. Hot-spot analyses revealed the environmental conditions controlling their propagation in the investigated area and provided an insight into the next 50 years in the age of global warming.

2 | METHODS

2.1 | Study area

The study area covered the region of the WAP and South-West Atlantic sector of the Southern Ocean (Figure 1). The waters flowing around the Antarctic Peninsula (AP) are a specific and unique mixture of various water masses (Martinson et al., 2008). Warm and

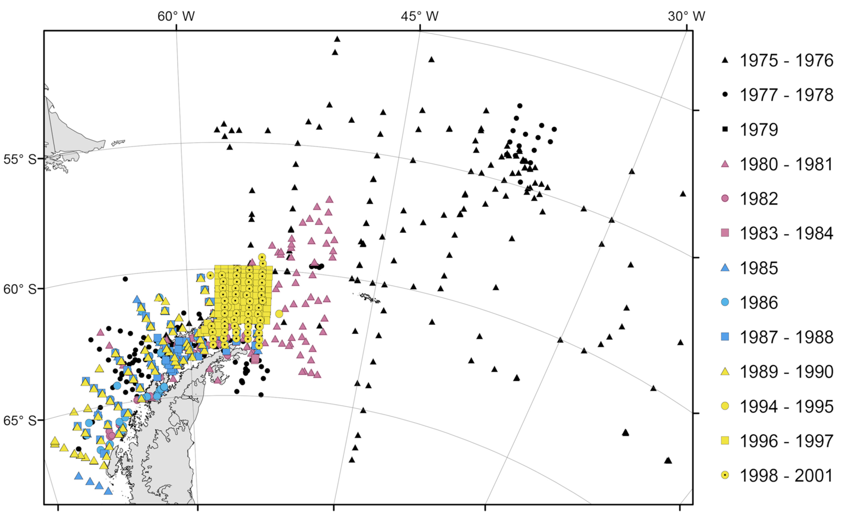

FIGURE 1 The locations of the sampling stations with the year of the cruise depicted in different colours and shapes

nutrient-rich Circumpolar Deep Water (CDW) mixes with cold Antarctic shelf and coastal water masses, having important effects on physical (e.g. sea ice extent and duration) and biological processes (e.g. primary production) (Ducklow et al., 2012). Antarctic Peninsula water mass distribution is restricted by bathymetric features such as continental slope, coastal, or shelf regions (Martinson et al., 2008). This region is also more susceptible to the influence of the ACC than other regions around the Antarctic where the ACC is rather distant from the shelf, typically separated by a polar gyre (Martinson et al., 2008). The marine ecosystems of the studied area are characterized by high diatom concentrations and, consequently, by high primary production, krill predominance, and a variety of predators (Siegel, Skibowski & Harm, 1992).

2.2 | Sampling

Samples 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 8 m^2) (Baker, Clarke & Harris, 1973) between 1975 and 2001, during early summer/late autumn (some years were not covered by the sample collection). The RMT8 was equipped with a real-time depth recorder 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 at a tow speed of 0.5–2.5 knots. 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, Hermann & Kühn (1982). All survey samples were processed at sea.

In total, 1,872 samples were collected from which salps were removed immediately after the tow, counted prior to other sample processing, and stored in 4% buffered formaldehyde for later measurements. Water temperature (T) and salinity (S) were measured prior to sampling (upper 200 m). However, these data were available only for a limited number of samples (i.e. 461 and 212 samples for T and S, respectively). Ice coverage was estimated from the bridge of the vessel by visual observation and by checking the radar, assessing the ice extent for more than one nautical mile around the vessel. Ice coverage was expressed according to % coverage in four classes: 0, 1, 2, and 3, representing no ice, <15%, <50%, and >50% ice cover within a one nautical mile radius, respectively.

2.3 | Reanalysis datasets

Water temperature and salinity were not measured *in situ* during all sampling surveys. Missing T data were complemented using the available complete monthly Sea Surface Temperature (SST) dataset. Because persistent cloud cover limits available satellite information in the Antarctic area, results of HadISST1 reanalyses published by the Met Office Hadley Centre for Climate Prediction and Research were used. Data collected in the Met Office Marine Data Bank had been quality controlled (e.g. corrected for bias and gridded onto a 1° area grid) (Rayner et al., 2003). Information about sea ice cover was obtained from the National Snow and Ice Data Center. The Sea Ice Extent data (ID: G02135) included in this study were downloaded in the form of complete time-series from November 1978 to the present, which were created at the Goddard Space Flight Center. Sea ice information was derived from passive microwave satellites, the Nimbus-7 Scanning Multichannel Microwave Radiometer, Special Sensor Microwave/Imager from July 1987 onwards, and Special Sensor Microwave Imager/Sounder instruments on board satellites launched as part of the Defense Meteorological Satellite Program. Data covered the Southern Hemisphere and were bounded to the north by the 39.23°S parallel at a spatial resolution of 25 × 25 km (Fetterer et al., 2017). Sea ice presence was expressed in a dichotomic (binary) way, where 1 and 0 referred to sea ice cover presence and absence, respectively. The ice sheet threshold was adopted as the point where the average sea ice concentration in that month dropped below 15%, which was consistent with the operational definition presented in the Intergovernmental Panel on Climate Change (IPCC) reports (Vaughan et al., 2013; Fetterer et al., 2017).

2.4 | Data analysis

To test possible correlations between significant environmental variables, non-parametric Spearman's rank-order correlations were calculated prior to analyses. Owing to the log-normal distribution of the data, further analyses were performed on the log-transformed abundance data [x' = log (x + 10)] using STATISTICA 12.0 PL (Statsoft Inc.) software. To reveal if sea ice concentration during sampling and in the preceding winter season (reanalysis dataset) had any impact on the number of salps during the following Antarctic summer, analysis of variance (Kruskal-Wallis test) and a probit regression model were used, respectively. Additionally, Generalized Additive Models (GAMs, Poisson distribution) implemented in CANOCO 5 software were used to examine the response of salp abundance by determining their most probable spatial distribution in relation to SST, bottom depth, and S, which were tested separately owing to the varying number of available *in situ* measurements of bottom depth, T, and S (1872, 461, and 212 samples, respectively).

2.5 | Spatial analyses

Global Moran's I statistic was used to test whether data were dispersed or for similarity between the collected samples, because it assesses the spatial autocorrelation based on values and features locations. Z-score statistics, representing measures of standard deviation, and *p*-values were computed along with the index to estimate statistical significance. A positive Moran's I index value indicates existence of clusters, whereas a negative one shows tendency toward dispersion (Moran, 1950). As the statistics pointed to strong data clustering (z-score > 60, *p*-value < 0.01), they were divided into three subsets based on decadal time periods. The division was based on the spatial distribution of sampling points, as the research stations were placed over a vast area and were confirmed as being statistically significant (z-score > 98, *p*-value < 0.01). Therefore, both ice cover interpolation and hot-spot analysis were applied separately to each decade (1970s, 1980s, and 1990s, including 2001 because of its similarity to the cruises from '94/'95 and '96/'97). To interpolate ice coverage, the Kernel Interpolation with Barriers method was performed, with the AP coastline from the Antarctic Digital Database 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 (Getis & Ord, 1992). The Getis-Ord Gi* statistic was chosen over more global statistics (e.g. Global Moran's I Index) to identify more local spatial clusters by finding local maxima, allowing comparison of each feature with surrounding neighbours (Getis & Ord, 1992). This analysis computes a z-score and *p*-value by default. High z-score and small *p*-value indicate clustering of high values (hot spots), while low z-score and small *p*-value indicate spatial clustering of lower values (cold spots). Point data were exploited to detect the hot-spot areas with significantly high salp densities and cold spots with low abundance. An inverse distance band was used to ensure that every point was used in the analysis in the decadal subsets.

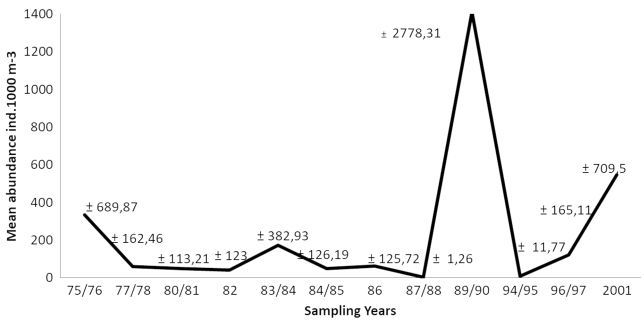

FIGURE 2 Mean abundance of *Salpa thompsoni* sampled each year (standard deviation values are given above the line)

The future boundary of temperature optimum for salp distribution range was established based on HadISST1 data from the Met Office Hadley Centre (Rayner et al., 2003). Mean distribution of surface temperatures during local summer (from December to the beginning of March) was created by mosaicking SST rasters for 1970–2001. The first boundary of salp occurrence based on thermal preferences was determined by extracting the periphery of the 0°C isotherm, and the temperature range for salp occurrence was based on available literature data (Foxton, 1966; Ono & Moteki, 2013; Henschke & Pakhomov, 2018). The predicted boundary after a temperature increase of 1°C was extracted analogically from the periphery of the 1°C isotherm. The simulation of future SST was conservatively based on the assumption that, if the water temperature recorded around Antarctica in the past 50 years increased by 1°C at a steady rate, SST will increase analogously in the next 50 years. This information was supported by the record of IPCC and measurements and results of *in situ* studies carried out for SST recorded by Meredith & King (2005). The maps presenting spatial distribution and abundances of *S. thompsoni* were created using ESRI® ArcMap™ 10.5.1 software.

3 | RESULTS

The extended collection comprised 1,872 samples, of which *S. thompsoni* was present in 1,278. The long-term data series revealed significant annual variability in salp abundance. Through the late 1970s and early 1980s, mean abundances of *S. thompsoni* were relatively low, with the exception of the cruises in '75/'76 and '83/'84. After the '87/'88 season with very low salp densities (0.9 ± 1.26 ind/1000 m^3), an extremely high abundance peak occurred in the summer of '89/'90, with a mean density of 1,408 ± 2,778.31 individuals/1000 m^3. Although the '94/'95 season was characterized by low salp abundances (6.3 ± 11.77 ind/1000 m^3), their numbers began to increase over the following years (Figure 2).

Analysis based on *in situ* data also confirmed that the high abundance of salps was influenced by sea ice concentration at the time of

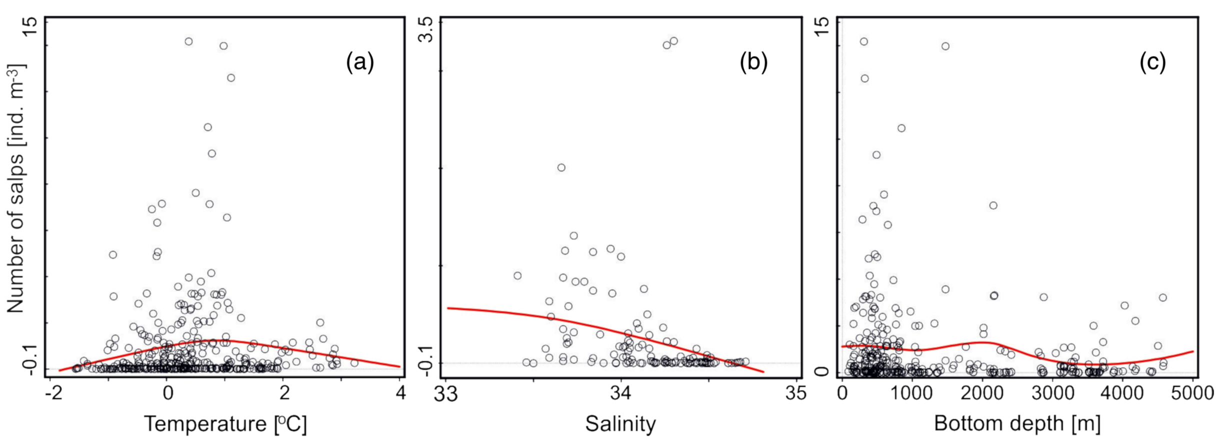

FIGURE 3 Generalized Additive Models (GAM) fitted for the number of salps against: (a) sea surface temperature (*N* = 461), (b) salinity (*N* = 212), and (c) bottom depth (*N* = 1,278)

sampling (Kruskal-Wallis test H = 33.98, $p < 0.0001$). Sea ice played a crucial role in Antarctic salp distribution, and significant differences were observed between stations without ice cover (category 0) and those with ice presence (categories 1–3). Interestingly, the probit model for the Sea Ice Index data confirmed that ice concentration during winter months (July and August) had a significant impact on the presence of salps the following summer season (N = 1,311, χ^2 = 211.36, $p < 0.0001$). The non-parametric Spearman's rank-order revealed only weak correlations between selected environmental variables (bottom depth vs T, rs = 0.2; bottom depth vs sea ice, rs = –0.25, and sea ice vs T, rs = –0.16). Therefore, GAMs (Figure 3) were tested independently and separately for the different environmental variables. The GAM including SST (F = 5.3, p = 0.0054) showed a unimodal response, with the highest number of *S. thompsoni* registered in the water layers at –1 to 1°C (Figure 3). GAMs including salinity (F = 5.8, p = 0.0039) or bottom depth (F = 15.0, $p < 0.00001$) did not show such a clear response. The highest numbers of salps seemed to be observed within waters of around 33.5–34.25 salinity, and the same model used for bottom depth showed the highest numbers of salps in the shallow shelf waters, with a depth of around 0–1,000 m (Figure 3).

3.1 | Hot-spot analysis

Despite the fact that sampling sites in the 1970s were spread along the west AP 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 (z-score > 1.67 and $p < 0.05$). In the 1980s, a hot spot was registered further to the south. Regardless of the similarity between sampling coverages of the WAP area, hot spots (z-score >1.7 and $p < 0.05$) were located in regions of the Biscoe Islands as well as Anvers Island and through the Bransfield Strait (Figure 4). Stations with high abundance of salps were located in areas with ice coverage classified as 1. Sampling stations in the '94/'95, '96/'97, and 2001 seasons were clustered around the Elephant Island region. This region showed *S. thompsoni* hot spots, with high z-scores (up to 7.89) and $p < 0.05$ (Figure 4).

4 | DISCUSSION

There was significant annual variability in *S. thompsoni* density owing to differences in bottom depth and environmental conditions (e.g. water temperature or ice condition) prevailing during sampling

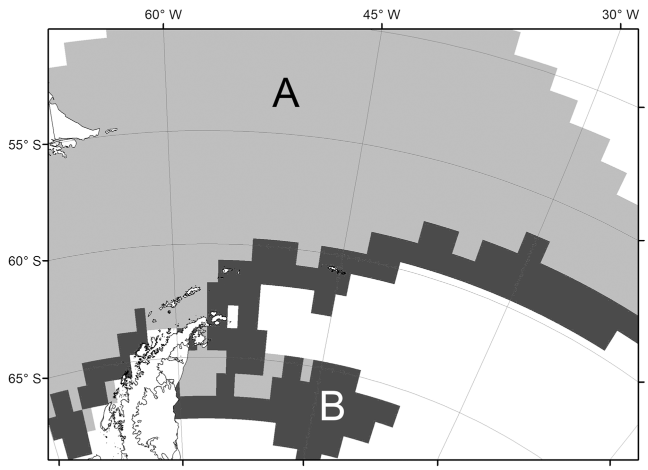

FIGURE 5 Boundary of *Salpa thompsoni* temperature optimum: in the studied year (A - marked in light grey) and prognosis on its change after 1° C temperature rise (B - marked in dark grey)

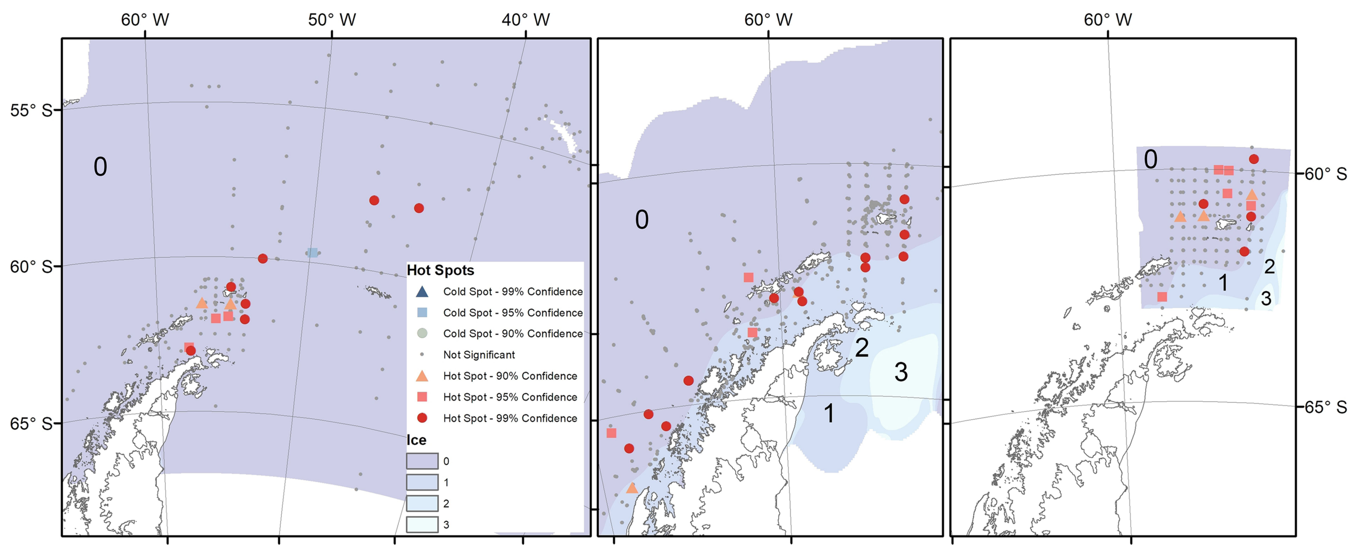

FIGURE 4 Hot spots of *Salpa thompsoni* distribution in decadal time series: (a) '70s, (b) '80s, and (c) '90s (in the background - the interpolated ice concentration for the respective time series. Cold spots marked: in grey circles - 90% confidence, blue squares - 95% confidence, dark blue triangles - 99% confidence; hot spots marked: in orange triangles - 90% confidence, dark orange squares - 95% confidence, red circles – 99% confidence; different sea ice degrees marked in: violet – without sea ice, dark blue – 1, sky blue- 2, light blue – 3)

years. Results showed that mild conditions during wintertime (July and August) with a lack of sea ice presumably allowed these animals to reproduce more efficiently and form larger and more condensed aggregations during the following summer period. Other studies conducted in previous years have revealed that dense salp aggregations were most frequently present in ice-free regions (Chiba et al., 1999; Atkinson et al., 2004; Lee et al., 2010; Mackey et al., 2011; Ross et al., 2014; Steinberg et al., 2015). However, our analysis showed that *S. thompsoni* may be present even with less suitable ice conditions (i.e. 15–50% of ice cover), so they might temporarily exist in colder environments. GAMs also showed that high salp density was located in shallow shelf waters (bottom depths 0–1,000 m), with low temperatures (−1–1°C) and salinity between 33.5–34.25 (Figure 3).

According to Atkinson et al. (2004), salps mostly prefer warmer water masses than do krill and occur in open waters with lower chlorophyll *a* concentrations and smaller phytoplankton particles, ideally between 4 and <0.05 μm (Madin, 1974; Atkinson et al., 2004). Therefore, they believed that cold shelf water is occupied only by Antarctic krill and will not be preferred by Antarctic salps, although, the current results seem to contradict this thesis. It should be noted that Atkinson et al. (2004) presented data series from the 1926–1951 period, whilst the samples for the current study were collected several decades later, between 1975 and 2001.

Our findings may suggest that the salp distribution range has increased and that they may occupy previously non-preferred areas. Their expanded occurrence range may be partially explained by the dynamics and distribution of ACC water masses, which are their natural environment, and may transport them over long distances close to the Antarctic continent. The ACC pumps warm (>1.5°C), salty (34.65–34.7), and nutrient-rich CDW onto the continental shelf below 200 m (Klinck et al., 2004). Another sign of salp transport to more southern areas was suggested by Henschke & Pakhomov (2018), demonstrating that *S. thompsoni* individuals were found at temperatures ranging from −1.85 to 8.57°C, with the highest abundances at 3–5°C, but also finding dense and mature populations at high latitudes. Thermal preferences were also previously confirmed by Słomska et al. (2015): *S. thompsoni* create massive aggregations in warmer waters (preferably 4°C) because it supports their fast and efficient reproduction processes. Annual and seasonal discrepancies in salp abundances and distribution records can vary yearly, which is associated not only with climatic fluctuations, but also with different sampling stations and methods (Atkinson et al., 2017).

Hot-spot analysis in three decades (the 1970s, 1980s, and 1990s) confirmed that *S. thompsoni* were distributed mostly around Elephant Island (61°08′S, 55°07′W). In the 1970s and 1990s, the largest numbers were located mostly in the open ocean as well as around the AP region. However, *S. thompsoni* hot spots in the 1980s were located evenly near the islands around Bransfield and Gerlache straits (64°30′S, 62°20′W), as well as far south near the Bellingshausen Sea (71°0′S, 85°0′W) with sea ice presence and lower water temperature. Our hot-spot analysis also showed that the largest number of salps was recorded between 60° − 70°S in the presence of ice cover and water temperature below 0°C, as in previous observations conducted by Ono & Moteki (2013), showing that a high number of mature individuals could be observed even south of the SB. Our results, together with those of Ono & Moteki (2013), have revealed that *S. thompsoni* appear across the SB of the ACC.

Comprehensive data about modification of the salp and krill populations presented by Ross et al. (2014) showed that krill abundance had decreased in the northern regions of the WAP and had shifted 200 km to the south. Our results complement and expand foregoing knowledge about the dynamics of Antarctic salp populations and demonstrate possible future salp distribution modifications under the assumption that water temperature will increase by 1°C. Additionally, our study showed that the *S. thompsoni* range could move southwards by an average of 200 km. Taking into account ongoing climate fluctuations, we tracked the movement of the temperature boundary for salps in a hypothetical situation of ocean warming by 1°C during the next 50 years (Figure 5). Comparing the positions of 0 and 1°C isotherms revealed that massive blooms of *S. thompsoni* may shift their distribution southward (e.g. 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 possibly exclude Antarctic krill, consequently leading to changes in the functioning of the Antarctic ecosystem.

Further research should focus on whether salp occurrence far into higher southern latitudes is periodic and related to the movements of ACC water masses, and whether climate change will be conducive to permanently extending their distribution ranges. Several genetic studies have revealed that extremely dynamic salp mitochondrial and nuclear DNA result in fast evolutionary rates, which suggests that salps have a high potential for adaptation to various environments (Goodall-Copestake, 2016; Jue et al., 2016). Thus, it is crucial to know how much they can adapt to these harsh environmental conditions, how much their physiological processes and life cycle are inhibited, and whether some degradation of their DNA occurs.

Our discovery of the southern salp population dynamics, together with previous observations (e.g. Ono & Moteki, 2013; Ross et al., 2014; Henschke & Pakhomov, 2018), can confirm that coastal salp populations might persist in cold shelf waters area, probably because of warming, which is an alarming signal for the Antarctic ecosystem. Considering the krill decline in the investigated region (Hill et al., 2019), predicted changes in salp abundance and distribution may consequently lead to changes in the occupation of the Antarctic krill feeding ground, have negative long-term consequences, and trigger a cascading effect in the Antarctic food web. Signs of salp ecological and genetic plasticity, as well as the prediction of further salp invasion, can be concerning, and the type of information provided in this study might be used to enable conservation of the Antarctic ecosystem and its inhabitants.

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AUTHOR CONTRIBUTIONS

All listed authors have made a significant contribution to this paper according to the following:

AW. Słomska - funding acquisition, investigation, visualization, writing - original draft

A. Panasiuk- supervision, writing - review &editing

J. Wawrzynek- analysis preparation, software

A. Weydman- data analysis, software

M. Konik- resources

V. Siegel- resources

The authors accepted and confirmed their participation before.

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