Environmental conditions for the successful development of *Salpa thompsoni* (Tunicata: Thaliaceae) blastozooids and embryos in the Atlantic sector of the Southern Ocean

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**Abstract**

Numerous studies have revealed that large numbers of gelatinous invertebrates, *Salpa thompsoni*, are reported more often in high-latitude Antarctic waters (> 60°S) than were reported in data obtained from the early twentieth century. Previously published studies also suggested that this tunicate may form a small subpopulation in cold shelf Antarctic waters. However, many researchers claim that harsh environmental conditions inhibit the reproduction and development of this species. Therefore, the aim of this study was to examine *S. thompsoni* blastozooids and the development ability of their embryos within different zones of the eastern and western parts of the Southern Ocean. The samples used in this study were collected from two transects, (I) between the Weddell Sea and coastal waters of South Africa and (II) between South America and the South Shetland Islands (Drake Passage) during the summer season of 2009/2010. The presented results showed that the highest likelihood for the presence of mature salps is observed under both in the conditions considered favorable that are characterized for mid-latitude areas as well as those observed at higher latitudes in the Antarctic zone (60°S) of the Southern Ocean. This work indicated that the prevailing environmental conditions in the Antarctic zone were distinguished by the highest diversity of embryo development stages and the densest salp aggregations. Our work revealed evidence for dualistic environmental preferences, while blastozooid development and embryo fertilization were equally successful at lower temperatures and low chl-*a* concentrations as well as when these variables reached higher values. This study expands the knowledge about environmental preferences and provides evidence for flexibility of salp reproduction, which allows it to adapt to various environmental conditions of the Southern Ocean.

**Keywords** Southern Ocean · *Salpa thompsoni* · Reproduction efficiency · Embryo development · Environmental preference · Limitations

**Introduction**

The Atlantic sector of the Southern Ocean straddles the largest environmental gradients in the world oceans and, therefore, provides a robust research location for environmental variability and biodiversity studies. The current phenomenon of environmental stress observed in the Southern Ocean, which is caused by climate fluctuations and human pressures may modify the structures, life cycles and reproduction of marine zooplankton (Beaugrand et al. 2009, 2015; Burrows et al. 2011, 2014; Gutt et al. 2015). In view of the above, studying the population structures of keystone Antarctic species is crucial for providing geospatial knowledge regarding biodiversity in the Southern Ocean.

The pelagic tunicate, *Salpa thompsoni* is a very common and abundant species in the Southern Ocean that has a wide circumpolar distribution, driven mostly by the waters of the Antarctic Circumpolar Current (ACC) (Foxton 1966; Pakhomov and McQuaid 1996; Pakhomov and Froneman 2004; Słomska et al. 2015). The exceptional life cycle of Antarctic salps is characterized by alternation of hermaphroditic, blastozooid and asexual oozooids which reproduce by strobilation (Foxton 1961; Daponte et al. 2001). Under favorable
environmental conditions, one oozooid may produce up to 800–900 juveniles, which leads to dense blastozooid blooms and predominance of Antarctic zooplankton assemblages (Daponte et al. 2001; Von Harbou 2009; Słomska et al. 2015). *S. thompsoni*, in contrast to Antarctic krill, stands out because it responds positively to warmer water temperatures, with significant increases in its numbers, and alternations in population structures and demographic profiles recorded over the past decades. Previous studies stated that *S. thompsoni* prefers warmer (> 2°C) and salty (~34.7) water masses with balanced chl-a concentrations (Pakhomov and Hunt 2017) and the SB is considered a barrier to successful reproduction by *S. thompsoni* due to its low temperatures and insufficient food concentration, which drive the breakdown of *S. thompsoni* populations (Casareto and Nemoto 1986; Chiba et al. 1999; Pakhomov et al. 2002; Ono et al. 2010; Ono and Moteki 2013). However, most recent studies have provided evidence that *S. thompsoni* is found more often in high-latitude Antarctic waters (60–70°S) (Steinberg et al. 2015; Ono and Moteki 2017; Henschke and Pakhomov 2019; Słomska et al. 2021), and observed that some individuals were even capable of crossing the SB of the ACC and forming a smaller subpopulation (e.g., Henschke and Pakhomov 2019; Słomska et al. 2021). These findings implied that salps may be present in high-latitude Antarctic waters, suggesting the potential occurrence of *S. thompsoni* reproduction in hostile environmental conditions; however, the limitations of their preferences are still not clear.

This study presents information about the persistence and developmental preferences of *S. thompsoni* blastozooids in combination with temperatures and chl-a concentrations recorded in different zones of the Atlantic Sector of the Southern Ocean. Our research complements the findings of other scientists and demonstrates some dichotomous preferences of *S. thompsoni* blastozooids indicating their high reproductive flexibility.

### Materials and methods

#### Sampling and blastozooid analysis

Sampling was performed during a Russian expedition on the R/V *Akademik Ioffe*. (Fig. 1) along two studied transects:

- **Transact I (TIE)**—Weddell Sea and the coastal waters of South Africa (December 2009)
- **Transact II (TIW)**—the Drake Passage

![Fig. 1 Geographical positions of sampling stations, with the distinguished positions of the stations with *Salpa thompsoni* individuals, in December 2009 and January 2010 along two studied transects:](image-url)
transect I (TIE), located between the Weddell Sea and coastal waters of South Africa (December 2009) and transect II (TIIW), located between the South Shetland Islands and South America (Drake Passage) (January 2010) (Fig. 1). The stations were classified into several characteristic biogeochemical zones: station TIE-4 in the Southern Subtropical Cycle (SATG), stations TIE-2, TIE-3, in the southern subtropical convergence (SSTC-E), station TIE-1 in the Antarctic (ANTA-E); and in the major hydrological zones: station TIIW-5 in the Southern American continental zone (SACZ-W); stations TIIW-4, TIIW-3 in the Antarctic zone (AZ-W); and stations TIIW-2, TIIW-1 in the continental Antarctic zone (CAZ-W) (Fig. 1, Table 1), which were established by Demidov et al. (2012). Salp samples were collected at depths of approximately 43 m at speeds of 1–2 knots by preforming oblique tows using a Bongo net (250 μm and 500 μm mesh sizes and 0.25 m² mouth area), which allows gentler catching and does not affect body structures. The Bongo net was not equipped with a flowmeter; therefore, quantitative analyses could not be performed in this study. Surface water temperature and salinity measurements were obtained by CTD probes (e.g., conductivity, temperature and depth) on the rosette system. To evaluate the chl-α concentrations, water samples were collected by a Russian scientific team with an SBE-32 Carousel Water Sampler from the upper 200 m layer at the CTD stations. The chl-α concentrations were measured by standard fluorometric methods, and detailed information about the sampling and measurements are presented in the paper of Demidov et al. (2012). Immediately after sample collection, salps were preserved in a 4% borax-buffered formaldehyde solution for later processing. Salps were isolated from the samples and classified with respect to species level, form and stage of development. Several species of salps were recorded along both studied transects, including a typical Southern Ocean S. thompsoni (~ 80%), a cosmopolitan S. fusiformis (~ 6%), as well as Thalia spp (~ 14%) and Soestia zonaria (~ 0.04%) which are abundant in the South Atlantic and South Pacific. However only the first species was distinguished by its diversified population structure; therefore only S. thompsoni was considered for further analysis. The proportion of oozooids to blastozooids observed in the surface waters of the Southern Ocean during summer season was 98% to 2%. The significant dominance of sexual blastozooids was recorded at all sampling stations, while oozooids were recorded in limited numbers and only in the northern part of the Drake Passage (station TIIW-5). For this reason, only blastozooids were included for further processing. All blastozooids were appropriately measured considering their body lengths, from the oral to the atrial aperture L (OA) (oral – atrial length) (Lüskow et al. 2020). To classify the maturity of hermaphroditic salps, the embryo length, L (em) (embryo length), was measured. Assessment of blastozooid embryo development was performed using a 7–stage scale (Stage) including both female and male stages. Stages were called buds, 0, I, II, III, IV and V and considered the embryo size and morphology or the presence of a placental scar (SCR). Recently, released blastozooids without embryos were classified as females at stage 0, and maturing females with developing embryos were classified regarding the size and shape of their embryos as stages I–IV. Blastozooids with visible placental scars were classified as stage V (embryo was released) and were considered functional males. The development stage, X, was also determined, and defined as an empty blastozooid without an embryo inside the body.

**Table 1**: Environmental conditions recorded at each research transect located in the study area; transect I (E- eastern part of the study area)—Weddell Sea and the African shelf; transect II (W- western part of the study area) the Drake Passage

| Station | Chl-α concentration (mg m⁻³) | Temperature (°C) | Salinity | Zone west/east |
|---------|-----------------------------|-----------------|----------|----------------|
| TIIW-1  | 0.34                        | 0.45            | 33.85    | CAZ-W          |
| TIIW-2  | 0.32                        | 0.72            | 33.72    | CAZ-W          |
| TIIW-3  | 0.14                        | 1.45            | 33.63    | AZ-W           |
| TIIW-4  | 0.12                        | 1.91            | 33.71    | AZ-W           |
| TIIW-5  | 0.34                        | 7.01            | 33.86    | SACZ-W         |
| TIE-1   | 0.76                        | 2.83            | 33.69    | ANTA-E         |
| TIE-2   | 0.45                        | 11.20           | 34.24    | SSTC-E         |
| TIE-3   | 0.35                        | 10.80           | 34.54    | SSTC-E         |
| TIE-4   | 0.41                        | 18.76           | 35.59    | SATG-E         |

Transit I and Transit II include biogeochemical provinces: SSTC—Southern Subtropical Convergence, SANT—Subantarctic, and hydrological zones: CAZ—Continental Antarctic Zone, AZ—Antarctic Zone, SACZ—South American Continental Zone described in detail by Demidov et al. (2012)

**Statistical analyses**

To explore the differences in S. thompsoni development at various stations, the Margalef diversity index was calculated which attempts to compensate for the effect of various sample sizes. For further data examination, the methods and tools available in Statistica were used. The Shapiro–Wilk test revealed a nonlinear distribution model of the tested data and indicated the need to apply nonparametric statistics. To explore the differences between S. thompsoni blastozooid responses in regard to (1) presence/absence of salps, (2) body lengths (OA) (3) embryo lengths with respect to environmental variables, namely, sea surface temperature, chl-α, and salinity, the U Mann–Whitney test and one-way ANOVA on ranks were used. The Spearman rank correlation was chosen to reveal the relationships among environmental factors and (1) the presence of advanced stages of salp development, (2) salp lengths (OA) and (3) the embryo lengths.
The nonlinear estimation model of probit regression was used to evaluate the combination of significant environmental variables (e.g., thermal conditions and chl-a concentrations) and the maximum likelihood of the presence of an advanced stage of salp development. The probit regression model was based on presence/absence records in reference to the advancement of their development, where 0 indicates only juveniles (stage 0 and buds) and 1 represents fertilized and maturing embryos (stages I–V). Detailed information about *S. thompsoni* development preferences was presented on a contour triangular plot calculated by the least squares method, as well as using the scatterplots against the variables that had a significant impacts on blastozooid development, e.g., chl-a and temperature, categorized by stage of embryo development.

**Results**

In the investigated areas, *Salpa thompsoni* individuals were observed between their northernmost border in the subtropical convergence zone, as well as far beyond their southernmost limits in continental Antarctica, between latitudes 35–62°S. The densest aggregations of salps (e.g., 914 individuals, diversity index 7.66), with the most diverse population structure including buds, 0–IV, V-released embryos and empty (failed reproduction—1%), were recorded at the latitude 60°S in the Antarctic Zone (AZ-W, station TIIW-3) as well as at stations TIIW-5 (257 individuals, diversity index 6.59) and TIE-2 (275 individuals, diversity index 7.59), located in the South American Continental Zone (SACZ-W) and in the Southern Subtropical Convergence (SSTC-E) (Fig. 2). The eastern part of the Antarctic Zone (ANTA-E) was characterized by the presence of mature individuals, such as females with embryos at stage III, as well as stage V, which means that individuals with released embryos was considered functional males. The western and eastern parts of the study area were both characterized by a very low contribution of failed embryos, where only 1% were classified as empty, which was noted only at the most numerous and reproductively diverse station within the Antarctic Zone (e.g., station TIIW-3), as well as at the Southern Subtropical Convergence (station TIE-2) (Fig. 2).

The results of the Mann–Whitney *U* test indicated significant differences between the values of different environmental conditions (chl-a: \(Z = 2.96, p = 0.003\); temperature: \(Z = 7.63, p = 0.0000\); salinity: \(Z = 3.36, p = 0.0007\)) at stations where females with fertilized embryos were recorded. The nonlinear estimation model of multivariate probit regression showed that the maximum likelihoods of recording mature individuals of *S. thompsoni* might be possible in areas with different environmental conditions, with lower temperatures (0–2 °C) and low chl-a (01–02 mg m\(^{-3}\)) concentrations as well as at stations located within warm water masses with temperatures ranging between 4 and 10 °C with chl-a values of approximately 0.6–0.8 mg m\(^{-3}\) (Fig. 3). The Spearman rank correlation confirmed that the tested variables, such as the presence/absence of advanced stages of salp development preferences was presented on a contour triangular plot calculated by the least squares method, as well as using the scatterplots against the variables that had a significant impacts on blastozooid development, e.g., chl-a and temperature, categorized by stage of embryo development.

![Fig. 2](image_url)
development (including females and males) and the OA blastozooid lengths, were correlated with temperature ($R=0.3; \; p<0.005; \; R=0.25; \; p<0.005$, respectively); salinity ($R=0.21; \; p<0.005; \; R=0.20, \; p<0.005$, respectively); and chl-$a$ concentration ($R=0.18; \; p=0.001; \; R=0.19, \; p=0.000$, respectively), while the embryo lengths exhibited weak, negative correlations with environmental conditions (chl-$a$: $R=-0.25, \; p=0.009$; temperature: $R=-0.26, \; p=0.005$; salinity: $R=-0.17, \; p=0.008$), but these correlations might be valid only in narrow ranges. Further exploration of the presented dataset revealed that $S. \ thompsoni$ blastozooids reached their largest sizes under distinct conditions. Salps developed equally well at lower temperatures (1.5–2 °C) and within unproductive Antarctic waters (0.1–0.2 mg m$^{-3}$) as well as in warmer waters (6–10 °C) with chl-$a$ concentrations of approximately 0.5–0.7 mg m$^{-3}$ (Fig. 4). Moreover, the categorized scatterplots confirmed that especially stations located in the Antarctic zone (AZ–W) were characterized by the presence of individuals with a very wide range of body sizes, from buds and juveniles of approximately 3 mm to males with body lengths of 60 mm (Fig. 5). A wide range of various blastozooid stages with body sizes between 10 and 30 mm was also recorded in the warmer SSTC-E and SACZ-W zones. Salp aggregations represented only by numerous juveniles (buds) and freshly realized blastozooids with undeveloped embryos (stage 0) with body sizes between 3 and 7 mm were also broadly found in the investigated areas even at the southernmost (62°S) station (CAZ-W) with temperatures < 0.5 °C as well as at the northernmost station (SATG-E) with temperatures of approximately around 18 °C (Fig. 5). Moreover, our results also indicated some dichotomous preferences in regard to embryo growth, showing that the studied embryos reached larger sizes at temperatures of approximately 1–2 °C and low chl-$a$ concentrations (< 0.2 mg m$^{-3}$), as well as in warmer waters with chl-$a$ concentrations of approximately 0.4–0.5 mg m$^{-3}$ (Fig. 5). Mature females with larger embryos, classified as stage II or III (> 0.8 mm), were recorded regardless of the low chl-$a$ concentrations and lower temperature values ($T<1.5 \; ^{\circ}\mathrm{C}$) (Fig. 6), suggesting that their growth was not inhibited by the lower temperatures during summer season.

**Discussion**

This study focused on the environmental preferences for the maturation and successful development of $Salpa \ thompsoni$ blastozooids and their embryos with respect to temperatures and chl-$a$ concentrations. Due to dataset limitations, our observation may add to the current knowledge and findings presented in a previous study by Henschke and Pakhomov (2019) regarding blastozooid environmental preferences.

Considering previous literature in regard to the temperature influence on salp horizontal variability, it could be found that the warm water masses of ACC (2–3 °C) has restricted impact on $S. \ thompsoni$ latitudinal dispersal (between 45 and 55°S) (e.g. Foxton 1966). However, in this study, $S. \ thompsoni$ blastozooids showed a very wide distribution across
both studied transects in the Atlantic Sector of the Southern Ocean. Blastozooids were recorded in large numbers between latitudes 35–62°S, both in the cold and non-productive water masses of the Continental Antarctic zone (CAZ-W), as well as in the Southern Subtropical Cycle (SATG), with temperatures ranging from 0.45 to 18.76 °C. In contrast to the results of Henschke and Pakhomov (2019), the densest *S. thomsoni* aggregations with a higher diversity index were noted south of the SB (60°S) in the Antarctic Zone (AZ) of the Drake Passage within cooler (<1.4 °C) and non-productive water masses (chl-a<0.13 mg m⁻³) with a lower salinity (33.6) and with characteristics typical of Modified Circumpolar Deep Water (MCDW: T<1.8 °C, salinity <34.7) (Bindoff et al. 2000). The high numbers of juveniles as well as mature males and females recorded south of the SB confirmed the successful development of *S. thomsoni* blastozooids across latitudes regardless of unfavour conditions. Our study also revealed that the western and eastern parts of the study area were characterized by a very low contribution of failed embryos noted at the most diverse stations within the Antarctic Zone, as well as in the southern subtropical convergence, which was characterized by oligotrophic conditions (chl-a—0.14 mg m⁻³ and 0.45 mg m⁻³, respectively). It can be stated that 1% of embryo failures were probably not caused by temperatures but rather by low food concentration, as only with the sufficient amount of food embryos may develop properly (Purcell and Madin 1991). Presumably, insufficient amount of preferred food particles triggered higher mortality rates of *S. thomsoni* blastozooids as well as absorption of their embryos (Chiba et al. 1999; Purcell and Madin 1991).

The key findings of this study are the binary environmental preferences for *S. thomsoni* development. Blastozooids seem to create two separate groups where one prefers lower temperature (1–2 °C) and low chl-a (01–02 mg m⁻³) concentrations and the other prefers warmer water masses with temperatures ranging between 4 and 10 °C with chl-a concentrations of approximately 0.6–08 mg m⁻³. The study showed that the presence of advanced stages of salp development and OA blastozooid lengths were positively correlated with temperatures, and chl-a concentrations, which allows us to suppose that salp

**Fig. 5** The scatterplots showing the relation between OA length of *Salpa thompsoni* blastozooids and the chl-a and temperature combinations categorized by the studied zones. The blue dots indicate OA length measurements in relation to temperature and chl-a combination in different zones of the Southern Ocean.

**Fig. 6** The scatterplot showing the relation between the embryo length of *Salpa thompsoni* blastozooids with combination of varying chl-a (mg m⁻³) conditions and sea surface temperature (°C). The blue dots indicate actual embryo lengths measurements in relation to temperature and chl-a combination.
reach bigger male and embryo sizes when these factors reached higher values; however, it should be mentioned that mature females and males were also found in surface water masses with temperatures between 0 and 2 °C with low chl-a concentrations (<0.2 mg m⁻³), which indicates that *S. thompsoni* blastozooids were able to continue their development under unfavour conditions and within unproductive Antarctic waters. Moreover, the distribution of salp body lengths with a very wide range of embryo sizes might be evidence for the presence of several different blastozooid generations within 1 year. As stated by Pakhomov and Hunt (2017) under appropriate conditions, *S. thompsoni* blastozooids may reproduce constantly because a favorable environment supports their rapid and greater reproduction processes. In the investigated areas of *S. thompsoni*, embryos also showed some dichotomous preferences and reached larger sizes at temperatures of approximately 1–2 °C and low chl-a concentrations (<0.2 mg m⁻³), as well as in warmer waters with chl-a concentrations of approximately 0.4–0.5 mg m⁻³. According to the previous studies, embryo size is mostly related to the food availability, as only with a sufficient amount of food they can develop properly (Purcell and Madin 1991). Thus, in harsher environmental conditions, the longer juvenile oozooids are protected in parent organisms, and growing to bigger sizes (Chiba et al. 1999). However, this research shows that mature females with larger embryos, classified as stage II or III (> 0.8 mm), were recorded regardless of the presence of low chl-a concentrations and lower temperatures (*T* < 1.5 °C) (Fig. 5), suggesting that their development was not inhibited by the low chl-a concentrations below 0.2 mg m⁻³, at least, during the studied summer season. During the present study, numerous juveniles (buds) and freshly realized blastozooids with undeveloped embryos (stage 0) were recorded at the southernmost and northernmost stations, which probably defined the limits for effective development. Further blastozooid is controlled by environmental conditions and advection of deeper water masses of the ACC and modified deep circumpolar water (MDCW). According to the previous findings of Henschke and Pakhomov (2019), mostly juvenile blastozooids might be found in surface Antarctic waters year-round, because they might be transferred into higher latitudes along with warmer water mass intrusions of the ACC (Casareto and Nemoto 1986; Henschke et al. 2021). When *S. thompsoni* is more developmentally advanced, specimens may be found in deeper layers (Hardy and Gunther 1935; Foxton 1966; Gili et al. 2006); however, since we have only surface samples, we cannot fully discuss this subject or confirm this hypothesis. Moreover, due to the scarce dataset, we are not able to discuss the whole life cycle of *S. thompsoni* or its reproductive ability throughout the year but could present only some environmental preferences for *S. thompsoni* blastozooid development, which might be an effect of reproductive flexibility, allowing it to adapt to various environmental conditions.

### Outlook and perspective

During the last few decades, the western Antarctic region has been under the strong influence of climate change modifications, which has substantially impacted the population structures and reproduction processes of planktonic communities. These changes will undoubtedly promote *S. thompsoni* expansion into the Bellingshausen, Lazarev, Weddell and Ross Seas, and salps may become permanently established in more southern Antarctic waters. This process would imply changes in the functioning of trophic relations, changes in biochemical cycles, and other consequences that we are not able to predict at the moment.

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### Data availability

The datasets analyzed during the current study are available from the corresponding author on reasonable request.

### Declarations

#### Conflict of interest

The authors have no relevant nonfinancial or nonfinancial interests to disclose.

#### Ethical approval

All applicable institutional guidelines for the care and use of animals were followed.

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