Variability of *Salpa thompsoni* population structure in the Drake Passage in summer season 2010

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Abstract: Dynamic climate changes have become noticeable in recent decades, especially in the vulnerable region of the West Antarctic. The relatively simple food web of this area relies on krill – *Euphausia superba*. Presumably, as a result of climatic fluctuations, a decrease in the number of this crustacean has been recorded, followed by an increase in the population of the gelatinous zooplankter *Salpa thompsoni*. In the research presented herein, population and morphometric analyses of *Salpa thompsoni* have been conducted. Specimens for this research were collected from the Drake Passage, using a Bongo net in the summer season of 2010. It has been found that the horizontal distribution of this gelatinous zooplankter was significantly irregular (Kruskal-Wallis test, p < 0.001). In the northern part of the investigated area, both blastozooids and oozooids were recorded, which confirms the dynamic development of this species. The central part of the Drake Passage was characterized by the dominance of blastozooids, with embryos found at different stages of the development. Only in the region of the South Shetland Islands, the salpid population was characterized by reduced or even stopped reproduction. The immense reproductive efficiency observed in the *Salpa thompsoni* population was mostly induced by the favourable thermal conditions. These observations may suggest that the ongoing climat changes in the West Antarctic will promote the population expansion of this species.

Key words: Antarctic, planktonic tunicate, horizontal distribution, population structure, climate change.

Introduction

Most studies conducted in the Antarctic region have focused on planktonic crustaceans, with an emphasis on Euphausiacea and Copepoda (Schneppenheim and Macdonald 1984; Thomas and Ikeda 1987; Calbet *et al.* 2006) which represent im-

portant elements of the Antarctic food web (Nishikawa *et al.* 1995). However, presumably as a result of the ongoing climate change (*i.e.* increase in air and water temperature, shifts in the direction and velocity of wind), significant increases in the number of the pelagic tunicate *Salpa thompsoni* have been recorded (Pakhomov *et al.* 2002; Atkinson *et al.* 2004; Ono and Moteki 2013). This tendency also correlates with a decrease in the population size of krill, *Euphausia superba*, especially in the West Antarctic (Loeb *et al.* 1997; Atkinson *et al.* 2004; Lee *et al.* 2010). The escalation of this process may destabilize the Antarctic food web to a considerable degree (McClintock *et al.* 2008; Alcaraz *et al.* 2014). Such a forecast is based on the low nutritional value of *S. thompsoni*, which is not sufficient to fulfil energetic requirements of higher trophic levels (Dubishar *et al.* 2006; Dubishar *et al.* 2012).

Studies of *S. thompsoni* in the Southern Ocean are frequent, however they almost exclusively focus on the ecology and biology of this species (*e.g.* Foxton 1966; Pakhomov *et al.* 2011), leaving the population analyses with a simultaneous assessment of each specimen development rather neglected (*e.g.* Pakhomov *et al.* 2006). Since comprehensive inquiries in this field are very scarce, their intensification is of the highest importance and common interest, as they might also shed a light on the mechanisms of the ongoing restructuring of the polar trophic webs.

The undeniably varying population structure of *S. thompsoni* in the peculiar area of the Drake Passage was an objective of the herein presented research. By the implementation of morphometric analyses, we were able to assess the diversity of developmental performance of *S. thompsoni* and its relation to the abiotic components of the local environment, which enabled us to forecast the probable direction of this species' future population structure changes in the region.

Materials and methods

Study area. — The Drake Passage is well recognized for its peculiar hydrological conditions caused by the phenomenon of cyclonic circulation of oceanic waters. These conditions depend on wind strength, vertical water mass movements and bottom topography (Joyce 1978). The Antarctic Circumpolar Current (ACC – also called West Wind Drift) moving eastward, and its counter-current, *i.e.* the East Wind Drift, suddenly accelerate in the area of the Drake Passage (Rintoul *et al.* 2001). This occurs as a consequence of the narrowing of the basin, bordered by the Antarctic Peninsula and Cape Horn, which causes the shift in the direction of both currents, turning them northward (Toggweiler and Samuels 1995; Parish and Cassano 2006). As ACC keeps its eastward movement, the collision of two currents occurs, creating turbulences underlying the formation of Weddell-Scotia Confluence (Patterson 1980; Rintoul *et al.* 2001; Barnes *et al.* 2006).

The coldest water masses of the Drake Passage are located near the South Shetland Islands. The average annual surface temperature is usually between -1.9°C

and -0.4°C, while salinity is approximately 33.8 PSU (Sudre *et al.* 2011). In the central Drake Passage, the Antarctic Surface Water with slightly higher temperatures (1–2°C in winter, 3–5°C in summer) and similar salinity values can also be found (Knox 2006). However, water masses situated out of the Antarctic Convergence in the Subantarctic Zone are typically characterized by surface temperatures of about 4–8°C in summer, 1–3°C in winter and salinity of 34.5 PSU (Knox 2006).

Water masses in the Drake Passage are under immense influence of the Antarctic Circumpolar Current, which causes their mixing. The current forms a wide bow-like pattern which flows between 40° and 56°S (Rintoul *et al.* 2001). In the investigated area, the border lines of ACC are not constant and perform frequent spatio-temporal variations (Orsi *et al.* 1995).

Sampling methods. — Samples for this study were collected in the Drake Passage during a cruise on R/V *Akademik Ioffe* during the Antarctic summer. Sampling was performed with a Bongo plankton net (250 μm and 500 μm) at nine stations, marked with numbers, along a transect between the South Shetland Islands and South America, between the 2nd and 10th January 2010 (Table 1). Most of the samples were collected during the day at a depth of about 43 m at a speed of 1–2 knots, with an exception of stations 2302 and 2333, where sampling was conducted at night. Bongo nets have not been equipped with flowmeters, therefore the quantitative analysis could not be performed in this study.

Values of surface water temperature and salinity were registered by a STD probe. Immediately after sample collection, samples were preserved in a 4% borax-buffered formaldehyde solution in the seawater for later processing.

Laboratory analyses. — Salps exhibit two developmental strategies different in the presence of internal fertilization. Therefore, two forms of mature organisms can be distinguished: (1) a sexually reproducing, viviparous blastozooid and (2) an oozooid which reproduces asexually by budding juveniles on its reproductive organs. Those organs are called stolons and are responsible for producing numerous

Table 1

Location of sampling stations in the Drake Passage in 2010.

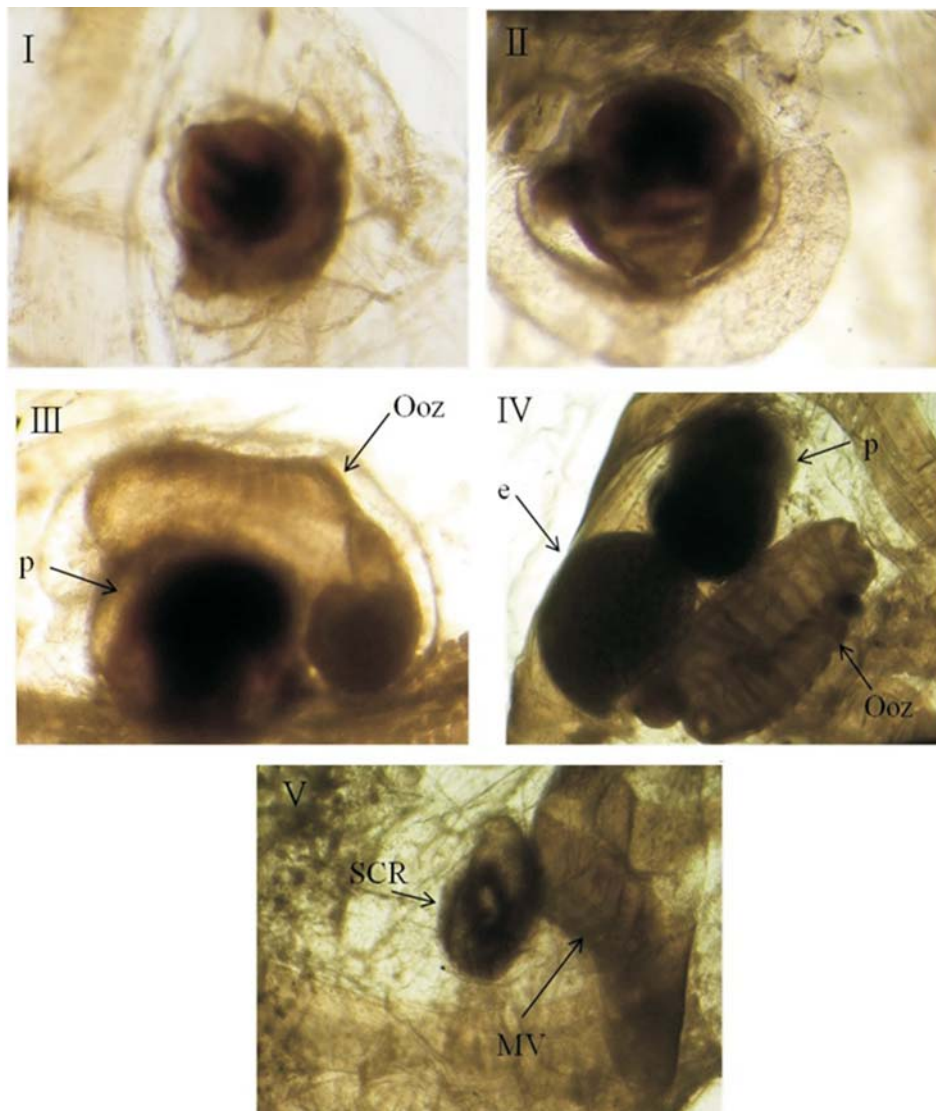| Station	Latitude (S)	Longitude (W)	Date
2284	62° 52'	62° 41'	02.01.2010
2288	60° 40'	63° 13'	02.01.2010
2302	60° 50'	64° 19'	04.01.2010
2305	60° 20'	64° 30'	05.01.2010
2311	59° 21'	64° 50'	06.01.2010
2317	58° 22'	65° 11'	07.01.2010
2323	57° 22'	65° 31'	08.01.2010
2329	56° 35'	60° 17'	09.01.2010
2333	56° 30'	60° 47'	10.01.2010

Fig. 1. Developmental stages of the blastozooid *Salpa thompsoni*: I–V – various stages of development, e – embryonic tissue, p – placenta, Ooz – embryonic oozooid, SCR – placental scar, MV – the fifth muscular band.

buds, which are organized into three groups of varying size (BI – first block, BII – second block, BIII – third block) (Loeb *et al.* 2012).

In addition to qualitative, morphometric and population analyses, all forms of salps were isolated from samples, however free embryos were not included in further processing.

The study of the development of *Salpa thompsoni* was conducted following the guidelines of Daponte *et al.* (2001), which included the determination of both

size and exact stage of the development of specimens. All the measurements fol-
lowed the criteria listed below:

1) for blastozooids – the length of the whole body from the oral to the atrial aperture
– L (OA) (Oral-Atrial Length) – was measured, as was the length of the whole
body from the dorsal appendix to the ventral appendix – L (T) (total length); the
size of embryo – L (em) (embryo length) was also determined (Daponte *et al.*
2001). Assessment of blastozooid embryo development was performed using a
6-stage scale (Stage), namely 0, I, II, III, IV and V, which takes into account the
size, the shape and the presence of placental scars (SCR) on embryos (Fig. 1);

2) for oozooids – the length of the whole body from the oral to the atrial aperture L
(OA) was measured, and the stolon's level of development was evaluated with
an additional measurement of each block length (B). Young buds (blastozooids)
developing on reproductive stolon blocks were counted and simultaneously the
oozooid stage of development was determined. The following characteristics of
oozooids were selected after Daponte *et al.* (2001) for the determination of their
development: the presence of scar, the number of blocks and buds on a stolon,
and the length of the block.

Data processing. — All the collected data have been analysed with Statistica
v. 10.1 software. Due to non-normal distribution of almost all data (Shapiro-Wilk
test, W = 0.453, p < 0.001), nonparametric statistics was used, whilst for the fur-
ther processing of temperature and salinity data (normal distribution), parametric
statistics was employed. In order to test the differences among samples at the level
of sampling station distribution, salpid development and population structure,
Kruskal-Wallis analysis of variance by ranks was performed. For environmental
data analysis, Student's t-test was used.

Results

Hydrological conditions in the study area. — Water temperature and salin-
ity were measured in the surface layers during the sampling. Due to normal distri-
bution of data, Student's t-test was performed, which confirmed the significance
of horizontal variability of both temperature (p < 0.001) and salinity (p < 0.001).
The lowest temperature was recorded at station 2284 (0.4°C) (Fig. 2). Thermal
conditions of the water definitely varied along the transect in the direction of South
America. The highest temperature was noted at stations 2329 and 2333, and
reached approximately 7°C (Fig. 2). The analysis showed that salinity distribution
throughout the investigated area oscillated between 33 and 34.

Horizontal variability. — Taxonomic analysis performed along the studied
transect showed specimens of only one species – *Salpa thompsoni.* Confirmation of
significant differences between each of the sampling stations in terms of the popula-
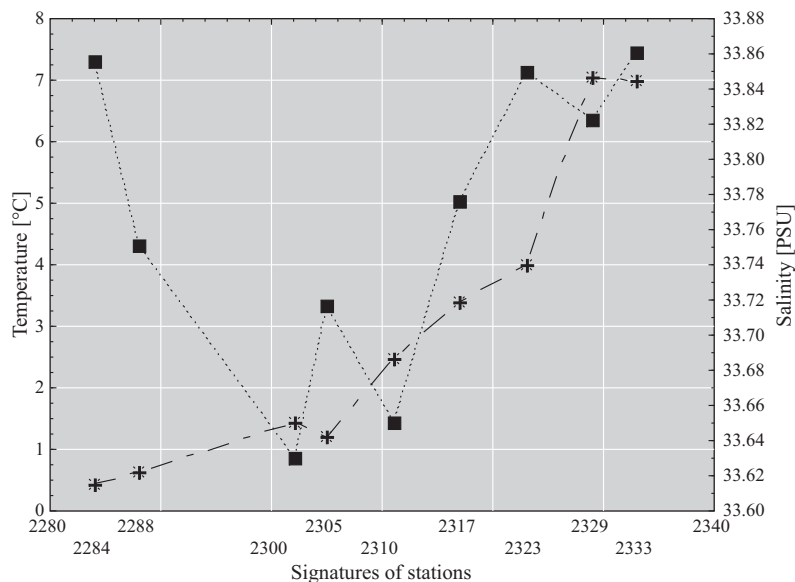
Fig. 2. Horizontal temperature (cross) and salinity variability (square) of surface water at sampling stations along the investigated transect.

tion structure and horizontal distribution of *Salpa thompsoni* comes from the results of the Kruskal-Wallis test (p < 0.001). The presence of this species was recorded only at five stations, four of which were near the southern border of the studied area (close to the South Shetland Islands – over 60°20' S at station 2305).

Population structure analysis of *S. thompsoni* performed during this study elucidated the dominance of blastozooids. This developmental form of salps represents 97% of all registered specimens. Oozooids were present only in the northern part of the Drake Passage (station 2333), while blastozooids were found near the South Shetland Islands and in the central and northern part of the investigated region.

The study also revealed that salps along the northwards direction of the transect were more developed, while at the southern, peripheral end of the transect, at stations 2284 and 2288 (Fig. 3), the majority of the registered specimens were blastozooid buds and blastozooids at early stages of the development (mostly 0). The most developmentally distinct stages of blastozooid's embryos occurred in the central region of the Drake Passage (station 2302, 2305). Salps determined as empty (stage X) were also present in the research area. Stage X constituted only one percent of all studied animals (Fig. 3).

A unique structure of the salpid population was found in the northern parts of the Drake Passage (station 2333) (Fig. 3) where both sexually (blastozooids) and asexually (oozooids) reproducing forms were equally numerous. However, a significant variability in their development progression was observed. Most of the oozooids found were at advanced stages (mainly 4a, 4b, 5a and 5b) (Fig. 3). More-
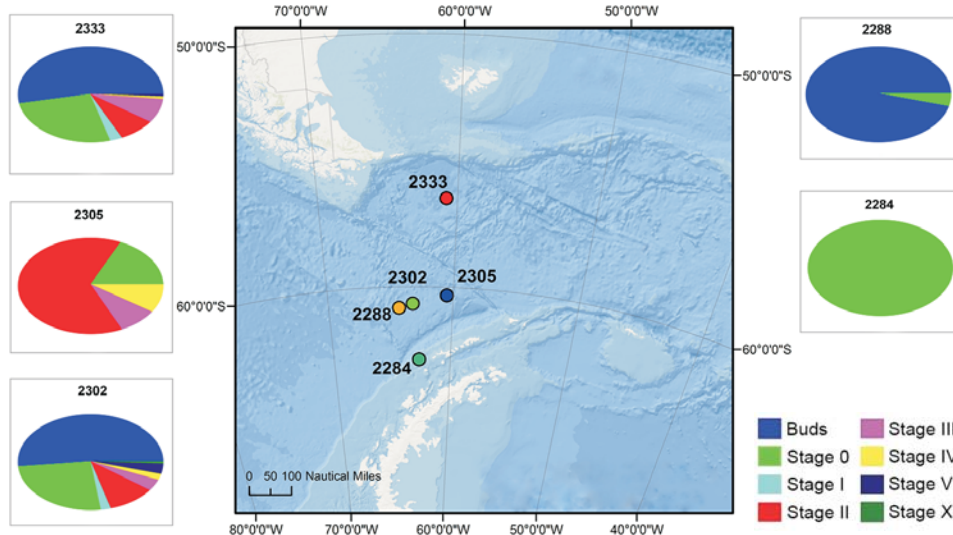
Fig. 3. Horizontal diversity of each stage of development, percentages of all development stages of *Salpa thompsoni* blastozooids in the Drake Passage.

over, presumably as a result of high reproductive activity of oozooids, most of the blastozooids found were just buds or small stage 0 specimens. As a result of the effective development of blastozooids, the oozooids at early stages (0, 1) were also frequently present in the sample (Station 2333) (Fig. 3).

Population structure and morphometric characteristics. — All forms of blastozooids were found in the investigated area, including adults (with embryos or a placental scar), blocks of juvenile buds, and young specimens just released into water (Table 2). Oozooids were recorded only at station 2333, in the form of single specimens or occasionally as free-swimming embryos.

Table 2

The average body length of *Salpa thompsoni* in the Drake Passage in 2010, with development stages taken into account; N – number of specimens found, L (T) – total length, SD – standard deviation, L (OA) – oral-atrial length.

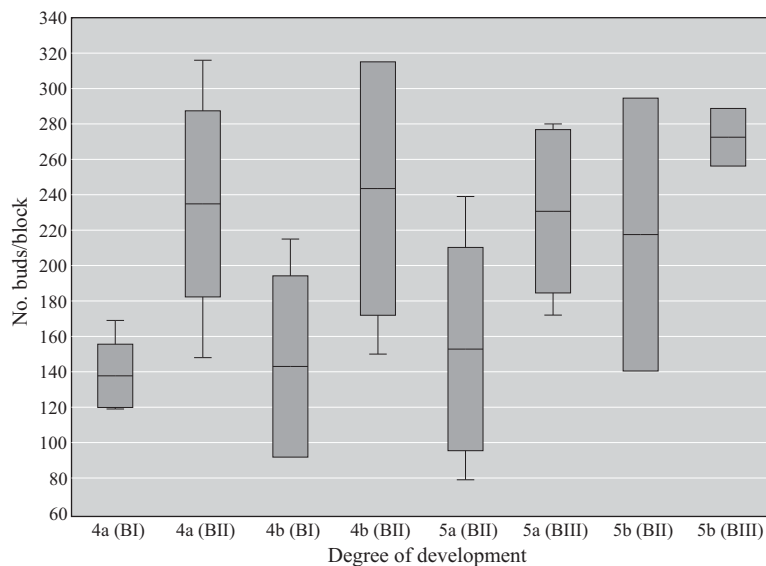| Stage	N	Average body length [mm]	
		L(T) ± SD	L(OA) ± SD
Buds	622	3.1±1.5	–
0	474	12.7±8.2	8.0 ±4.1
I	28	19.5±4.6	13.4±2.3
II	124	22.6±5.6	14.0 ±2.3
III	54	38.3±11.9	20.9±1.6
IV	22	43.5±9.4	24.7±5.4
V	32	39.4±6.8	21.4±3.5
X	8	23.1±5.0	20.5±5.4

Fig. 4. The average bud number within each block of stolons (BI – block I, BII – block II, BIII – block III), with stages of development of *Salpa thompsoni* oozooids in the Drake Passage in 2010, where boxes represent standard deviation values with minimal and maximal numbers of encountered buds presented as whiskers.

The analysis of *Salpa thompsoni* oozooids showed their high developmental diversity. The average number of buds inside the lower block did not exceed 200 specimens, while approximately 230 juvenile blastozooids were recorded in the upper block (Fig. 4). Altogether, on average 490 younger forms (stage 5b) could be found inside one oozooid (Fig. 4).

The morphometric analysis of oozooids of *Salpa thompsoni* revealed a varying length of this animal body. This parameter varied from 32 mm (stage 1) to 79 mm (stage 5b) (Fig. 5).

Populations of *Salpa thompsoni* were dominated by blastozooids at early stages of the development marked as 0 (474 of 760 specimens found). Embryos ranging in size from 0.41 mm to 2.43 mm (Fig. 6) were found in most of the adult blastozooids, leaving just a few of them, referred to as an empty stage (X) (Table 2). Buds of juvenile blastozooids had an average size of 3.1 mm (Table 2). The average body length [L (T)] of the biggest blastozooids exceeded 43 mm, while the smallest ones were about 12.7 mm long (Table 2).

Discussion

Horizontal variability. — Irregularities in the spatial distribution of *Salpa thompsoni* directly correlate with its life and reproductive cycle. Efficient oozooid reproduction, yielding 800–900 blastozooids each time, enables this gelatinous
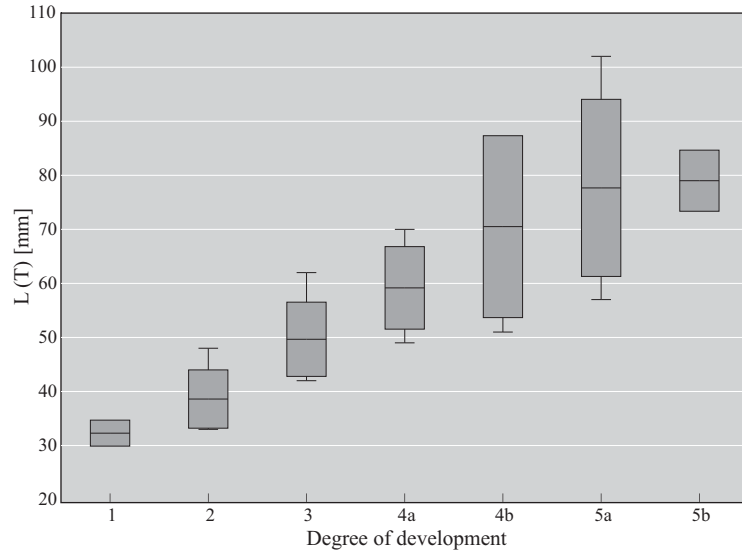
Fig. 5. The average body length of *Salpa thompsoni* oozooids recorded in the Drake Passage in 2010, sorted into individual stages of development, where boxes represent standard deviation and whiskers show minimal-maximal values
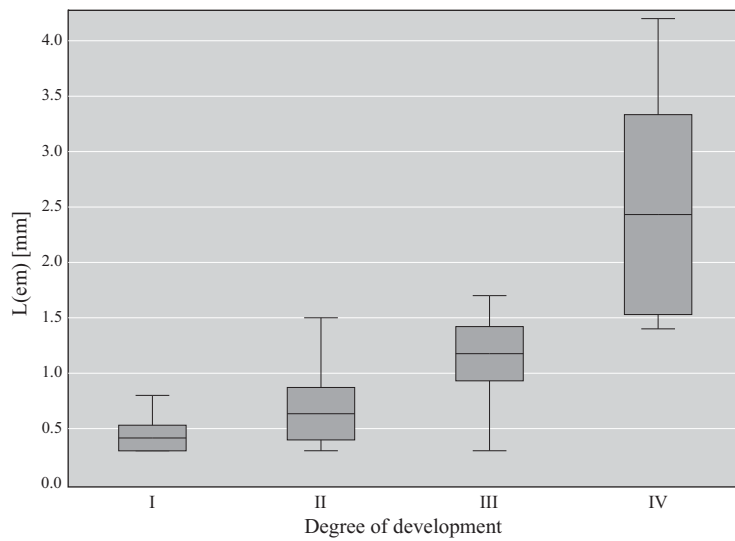

Fig. 6. Average size of blastozooid embryos of *Salpa thompsoni* in the Drake Passage in 2010, with individual stages of development taken into account, where boxes represent standard deviation and whiskers show minimal-maximal values.

zooplankter to form numerous, highly concentrated aggregations in relatively small areas (Pakhomov *et al.* 2006). However, those swarms of salps in the surface waters are random events rather than constant and predictable phenomena (Heron and Benham 1984).

Consistent with the literature data, the proportion of oozooids to blastozooids observed in the Southern Ocean seems to be uninterrupted in the long-term cycle (Loeb *et al.* 2012). Our results revealed 97% of blastozooids and 3% of oozooids. This is connected with the peculiar life cycle of Salpidae, and also with the reproductive strategy of both described forms. Asexually reproducing oozooids are capable of producing hundreds (200–300) of blastozooids in a single block, releasing up to four blocks per cycle (Daponte *et al.* 2001). Sexually reproducing blastozooids of *Salpa thompsoni* produce only one egg cell during their entire life cycle, from which only one oozooid develops (Nishikawa *et al*. 1995).

At lower latitudes, oozooids are capable of releasing blastozooids multiple times throughout the year. On the other hand, oozooids of *Salpa thompsoni* living at higher latitudes have a life cycle with only single releases of blastozooids (Loeb *et al.* 2012). The varied spatial distribution might be thus attributed to the fact that at lower latitudes summer starts earlier and lasts longer than it does at higher latitudes (Chiba *et al.* 1999). The consequence of this situation is the early reproduction of oozooids in the northern part of the study area.

The developmental ratio of *Salpa thompsoni* from this study is consistent with typical late-summer or early-autumn reproductive efficiency of this species (Chiba *et al.* 1999). In samples collected off the South Shetland Islands shores (2284 and 2888), only blastozooids with eggs not yet inseminated were found. The prevalence of those immature, viviparous forms is an indication of high reproductive activity of oozooids. However, almost none of the latter were present in the investigated area. There are two possible explanations of the absence of asexually reproducing forms. The first being the depth range of oozooids occurrence, which tends to live in deeper regions of the ocean, thus a relatively shallowly trawled net might have not encountered them. The second explanation takes the duration of the oozooid stage into account – salps of this region die soon after releasing blastozooids. There is also a possibility of an unfavourable temperature effect, namely cold temperature may cause a slower development (Chiba *et al*. 1999). However, this unfavourable impact of temperature was shown to be more influential for the blastozooids. Ono and Moteki (2013) found that blastozooids demonstrated a slowed development in temperatures ranging from 0.4–0.8°C, with a complete discontinuation or even reversing development (embryo absorbing) in far harsher environment (Chiba *et al*. 1999).

Considering temperature influence on salpid horizontal variability, one could easily find literature evidence for the restricted impact of warm water masses of ACC on those plankters latitudinal dispersal *e.g.* at 45–55°S (*e.g*. Foxton 1966). Contrary to the disadvantageous influence of low temperature on the reproductive efficiency, a rapid increase in the reproduction ratio can occur when temperature increases. Our findings confirm such an assumption as we found both blastozooids and oozooids reproducing actively in the northernmost part which remained under the influence of ACC, where temperature exceeded 2–3°C. Following a higher

temperature, the primary productivity of this region was also intensified (Demidov and Mosharov 2012), leading to conclusion that both temperature and food availability share a beneficial impact on salps.

Population structure and morphometric characteristics. — In this study, a detailed analysis of oozooid stolons was performed, and the results were compared with long-term data collected by Foxton (1966) in March over the period of 1925–1951, and by Daponte *et al*. (2001) in the Antarctic summer 1994/95 from the Weddell-Scotia Confluence. Different proportions of particular stages result from the fact that salps from waters classified as Subantarctic start their reproductive cycle earlier than those from cooler waters of the southern part of the Southern Ocean (Kawaguchi *et al.* 2004). Usually with the growth of oozooids, the possible number of juvenile blastozooids on stolons also increases. However, the biggest specimen recorded by Daponte *et al*. (2001) in 1994 measured 85 mm and produced about 375 buds, while the biggest oozooid recorded in this study measured 78 mm and had 491 buds (Table 3). This difference may be related to the fact that the rate of reproduction is defined not only by the body size, but also by the abiotic environmental components, like temperature and food availability (Heron and Benham 1984), thus it should be emphasised that Foxton (1966) and Daponte *et al.* (2001) conducted their research in March, at the end of the polar summer when environmental conditions might be far less favourable than those typical of the polar summer. To sum up, specimens of *Salpa thompsoni* analysed in the present research were characterized by higher reproductive abilities and more effective de-

Table 3

The average body length of *Salpa thompsoni* oozooids, and the number of buds on blocks, with individual development stages taken into account; comparison of results from this research and literature data. L (OA) – the average body length of an oozooid measured from the oral to atrial aperture, BI/II/III – the number of buds for each block.

	Stage	Foxton (1961)	Daponte (2001)		Current data
		March 1925–1951	March 1994	March 1995	January 2010
4a	L(OA)[mm]	58	62.50	59.5	58.4
	BI	118	125.1	119.3	137
4b	L(OA) [mm]	65	72.5	68.5	70.5
	BI	112	184.6	142	144
	BII	117	195	155.5	234
5a	L(OA) [mm]	68	77.5	73.3	77.7
	BII	132	200	171.6	153
5b	L(OA) [mm]	75	85	85.5	79
	BII	123	210	174.3	218
	BIII	231	13.3	200.6	273
6a	L(OA) [mm]	–	–	87.5	78
	BIII	–	–	232	220

Table 4

The average length of *Salpa thompsoni* blastozooids embryos at different stages of development – a comparison of our results with literature data.

Stage	Embryo length [mm]		
	Daponte (2001)	Harbou (unpublished)	Current data
I	1–2	0.3–0.9	0.3–0.4
II	2–3	0.5–1.9	0.4–0.7
III	3–4	1.6–2.5	1.1–1.4
IV	>4	2.2–7.3	1.8–5.4

velopment in comparison to specimens studied by Foxton (1966) and Daponte *et al.* (2001) in the Atlantic Sector of the Southern Ocean.

Body lengths of *Salpa thompsoni* blastozooids collected from the Drake Passage in 2010 were compared with those measured in 2004 (Harbou unpublished data), and also with those gathered during the Antarctic summer of 1994–1995 by Daponte *et al*. (2001) (Table 4). This comparison did not reveal any major differences. Blastozooids collected by Daponte *et al.* (2001) had the body length [L(OA)] ranging from a minimum of 5 mm to a maximum of 43 mm, while Harbou (unpubl. data) recorded sizes between 5 mm and 45 mm. The oral-atrial length of blastozooids in the present study ranged from 4.4 mm to 42 mm.

The size of embryos is related to the food availability, as only with the sufficient amount of food they can develop properly (Purcell and Madin 1991). Thus the harsher the environment becomes, the longer juvenile oozooids will be protected in parent organisms, growing to bigger sizes (Chiba *et al.* 1999). In our research only small embryos were recorded leading us to the conclusion that the summer season of 2010 was favourable for salps allowing them to reach the pre-release maturity at smaller sizes.

Conclusions. — The horizontal diversity of the population structure of salps in the Drake Passage is most likely a consequence of the water temperature fluctuations. The northern part of the area was characterized by a high value of this parameter, which presumably triggered off high reproductive activity of oozooids and blastozooids, while disadvantageous environmental conditions, such as water temperatures of approximately 0°C prevailing in the southern region of the Drake Passage, presumably caused slowed or reversed development of salps.

Salpa thompsoni present in the Drake Passage during the summer of 2010 had higher reproduction efficiency than the same species of Salpidae investigated in other studies (Daponte *et al.* 2001; Harbou unpublished data). It can be assumed that higher reproductive success was caused by a more favourable environment. It thus appears that the ongoing climate change in the susceptible region of the Southern Ocean will promote more effective development and thus contribute to an increase in the population size of this species.

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