Deep–Sea Research Part II xxx (xxxx) xxx–xxx

Contents lists available at ScienceDirect

Deep–Sea Research II

journal homepage: www.elsevier.com/locate/dsr2

Trans-Atlantic variability in ecology of the pelagic tunicate *Salpa thompsoni* near the Antarctic Polar Front

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ABSTRACT

The distribution, density, demography and feeding dynamics of the pelagic tunicate *Salpa thompsoni* were investigated during the trans-Atlantic ANTARKTIS XXVIII/3 expedition to the Southern Ocean, on board RV *Polarstern*, between January and March 2012. Net samples were collected using an RMT-8 at four major sampling regions in the proximity of the Antarctic Polar Front (APF): along a 10°E transect, Salpastan, 12°W eulerian study, and the South Georgia Basin. Salps, mostly *S. thompsoni*, were found at all but one station and with few exceptions contributed < <40% to total zooplankton in terms of both abundance and biomass. Salp abundance and biomass was lowest (6.2 ind.1000 m^{-3} and 0.8 mgDW m^{-3}) north of the APF along the 10°E transect and highest (3150 ind.1000 m^{-3} and 20.5 mgDW m^{-3}) at the Salpastan station south of the APF. Size distributions of *S. thompsoni* aggregates and solitaries, and their developmental dynamics, were similar in all locations except the Salpastan region. In aggregates, the overall salp size distributions were strongly right-tailed with the mass of the distribution always concentrated in the left where small aggregates (6–10 mm) dominated. During the eulerian study at 12°W, several cohorts of aggregates and solitaries were traceable allowing assessment of the daily growth rates of *S. thompsoni*. Estimated in situ growth rates of aggregates and solitaries were 0.53 ± 0.18 and 2.83 ± 0.42 mm day^{-1}, respectively, and the complete *S. thompsoni* life cycle duration (sexual+asexual) during austral summer at the APF region may have been as short as 2–3 months. The rapid growth rates of *S. thompsoni* found in this study urgently require further research to re-evaluate salp life cycle in the Southern Ocean.

1. Introduction

Pelagic tunicates are conspicuous members of the pelagic zooplankton community in many regions of the world ocean (Kashkina, 1978; Madin and Diebel, 1998; Henschke et al., 2016). They are known to be well adapted to oligotrophic systems being extremely efficient at capturing food particles in submicron to mm size range (Bone et al., 2003; Kremer and Madin, 1992). When conditions are right, pelagic tunicate populations may undergo explosive increases by means of asexual reproduction and fast growth rates (Foxton, 1966; Madin and Diebel, 1998), contributing significantly to primary production removal and vertical carbon flux through production of energy rich, fast sinking fecal pellets and senescent bodies (Pakhomov et al., 2002; Henschke et al., 2016; Iversen et al., it this issue). It appears that despite their low carbon content and overall nutritional value compared to the majority of crustacean plankton, pelagic tunicates are consumed by a variety of predators and may support unique yet not well studied gelatinous food webs (e.g. Kashkina, 1986; Andersen, 1998; Pakhomov et al., 2002; Henschke et al., 2016).

In the Southern Ocean, the most common and numerous species of pelagic tunicates is *Salpa thompsoni* (Foxton 1966). It is distributed from the Subtropical Convergence southward to the coastal Antarctic Sea's but is most abundant in the region of the Antarctic Polar Frontal Zone (Foxton 1966, Pakhomov et al. 2002, Loeb and Santora, 2012). Since the original work that described its general distribution and life cycle (Foxton 1966), *S. thompsoni* has received increased attention in recent decades mainly due to reports indicating its southward shift in distribution and overall increase in abundance in the high Antarctic (Chiba et al., 1998; Loeb et al., 1997; Pakhomov et al. 2002, Atkinson et al. 2004). Salps were suggested to reflect large-scale changes in the Southern Ocean ecosystem (Pakhomov et al. 2002, 2006) and possibly related to a dramatic decline in Antarctic krill, *Euphausia superba*, abundance (Atkinson et al. 2004). Although the relationship between these two species is still not clear and debated, increased emphasis on

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http://dx.doi.org/10.1016/j.dsr2.2017.03.001

S. thompsoni ecology has provided new insights into its general biology, including reproduction and life cycle (e.g. Daponte et al., 2001; Pakhomov et al., 2006, 2011; Loeb and Santora, 2012), distribution (e.g. Pakhomov et al., 2010; Ono and Moteki, 2013, 2016; Ono et al., 2010), metabolic rates (e.g. Pakhomov et al., 2006, Phillips et al., 2009; Von Harbou et al. 2011) and functional role (e.g. Dubischar et al., 2006, 2011; Henschke et al., 2016; Iversen et al., in this issue). It appears that salps still have a limited role in high Antarctic ecosystems due to the negative effects of low temperature on their development (Pakhomov et al., 2010, 2011; Ono and Moteki, 2013, 2016). This situation however may change if the Southern Ocean continues to warm due to climate change (Pakhomov et al., 2010; 2011).

The majority of previous studies investigating the biology of *S. thompsoni* have been localized and the only study at the basin or circum-Antarctic level remains to be the classic work of Foxton (1966) based on the Discovery Expedition collections. That study however often pooled biological data across the Southern Ocean with little consideration for longitudinal or basin wide variability in the *S. thompsoni* ecology. It was assumed that observations in distant habitats embedded into the continuous circum-Antarctic realm would be representative of the overall salp population dynamics because salp development at the large scale would have been synchronized by seasonal processes. While this may be a reasonable assumption based on the Southern Ocean regionalization attempts (Grant et al., 2006), the most recent genetic studies have shown that even within a single basin pelagic species may have higher diversity than anticipated based on gene exchange modulated by the Antarctic Circumpolar Current (e.g. Havermans et al., 2011; 2013). Overall, inter-basin comparisons of pelagic zooplankton ecology in the Southern Oceans are rare. Furthermore, the approach of snapshot surveys has potentially masked high temporal resolution population demographics and hindered assessment of salp growth rates. The main aims of the present study were twofold: first to focus on the large scale dynamics of the *S. thompsoni* ecology (distribution, biology and feeding) along the axis of the Antarctic Polar Front that may be related to longitudinal changes in the hydrological regimes; and second to assess salp developmental dynamics as well as growth rates during a high temporal resolution eulerian study in the vicinity of the APF.

2. Material and methods

Samples were collected during the “Eddy-Pump” Project in the Atlantic Sector of the Southern Ocean onboard the R.V. *Polarstern* during its ANTARKTIS XXVIII/3 voyage (Wolf-Gladrow, 2013). Sampling was conducted between January 11 and March 5, 2012 and concentrated in four main regions along the axis of the Antarctic Circumpolar Current in the proximity of the Antarctic Polar Front (APF) between 10°E and 41°W: 1) along a 10°E transect spanning the APF, 2) Salpastan, 3) a 12°W eulerian study, and 4) the South Georgia Basin (Fig. 1). The 12°W eulerian study was sampled every 2–3 days between January 31st and February 17th. Majority of these stations were centered at 51.20°S and 12.66°W with only two stations conducted slightly to the south-east (St. 86-19, January 31) and northwest (St. 139-6, February 15) (Fig. 1).

At each station vertical profiles of temperature, salinity and density were derived from measurements made by lowering a Sea- Bird Electronics SBE 911plus CTD (Conductivity, Temperature and Depth) to a minimum depth of 1000 m. The CTD and ancillary instruments were attached to a Sea-Bird SBE 32 Carousel multi-bottle water sampler holding 24 12-liter bottles (Strass et al., in this issue). In addition, subsurface chlorophyll-a (Chl-a) measurements were obtained from ~5 m depth by filtering 2 L of seawater through GF/F filters and placing the filter into 10 mL of 90% acetone with 1 cm^3 of glass beads. The samples were then stored at −20 °C for at least 30 min. Thereafter the samples were ground for 3 min and centrifuged at 5000 rpm at 0 °C. Chl-a was measured from the supernatant on a Turner 10-AU fluorometer.

Salps were collected using a rectangular midwater trawl type RMT-8+1 harnessed with 4.5 and 0.3 mm mesh nets. A flowmeter was mounted at the mouth of RMT-8 to measure volume filtered. The volume filtered by the RMT-8 varied between 10,000 and 24,000 m^3. Net tows were made at a speed of ~ 2.5 kt and completed as double oblique hauls in the upper 250 m of the water column mostly during darkness. Only four daytime stations, namely Stns. 60-6, 69-7, 128-13 and 136-10, and two dawn and dusk (162-1 and 176-1) stations were conducted. Salps were picked fresh from the entire sample or from ¼ to 1/32 sub-samples (depending on the catch size) and processed at sea. Salps were counted, separated into aggregate and solitary forms, staged and measured for body (oral-atrial distance, OA) length to the nearest millimeter according to Foxton (1966).

The maturity stages of *S. thompsoni* have been described in several papers (e.g. Foxton, 1966; Casareto and Nemoto, 1986; Chiba et al., 1999; Daponte et al., 2001; Pakhomov et al., 2011). Following these descriptions, the maturity stages of aggregates were determined according to the morphological characteristics of the embryo inside an aggregate body. Five different stages (from 0 to 4) were classified according to the gradual growth of the embryo. At stage 0, the ovarian sac is spherical with no sign of embryo development. By stage 4, the embryo, often > 4 mm in length, resembles in all features the early oozoid (see pictures in Foxton, 1966 and Daponte et al., 2001). Stage 5 or ‘spent’ was identified by the presence of a placenta scar, which indicated that the embryo has been released. Finally, we observed two very large aggregate forms: one with placenta scar and visible sperm channels on the salp nucleus, which were classified as male aggregates (M), and the other with no placenta scar and no clear visible sperm channels (NE), which were classified as potential male aggregates. The developmental stages of *S. thompsoni* solitary forms were determined according to the morphology of the stolon. Solitary stages 0 to 4A represent the development of the solitary from embryo release (0) to the first fully differentiated block (chain) of aggregates (4A) (Daponte et al., 2001). Stage 4B is the stage in which proximal aggregate block is developing, while the distal block is fully developed and ready to be released. At stage 5A, the first (stage 4B distal) block has been released and the second block is developing. The presence of a scar through which the first block was released permitted the distinction of stage 5A from 4A. Stage 5B has both blocks (proximal and distal) fully developed and the distal block is about to be released. According to Daponte et al. (2001), this process may continue until the budding capacity of the stolon is exhausted, passing through stages 6a and 6b and possibly beyond. In our study, however, we did not have means to distinguish stages beyond 5B.

To measure salp feeding activity, immediately after capture salp stomachs were dissected out and placed individually in plastic tubes with 10–50 ml (depending of the salp size) of 90% acetone and stored at −18 °C for 36 h. After centrifugation (5000 rpm), Chl-a and phaeopigments, were measured with a Turner Designs 10AU fluorometer, before and after acidification (Mackas and Bohrer 1976). Gut contents were expressed in terms of pigment equivalents (Chla-a+phaeopigments) per individual and calculated according to Conover et al. (1986). When the Chl-a/phaeopigment ratio of the gut content was higher than 0.25, total pigment levels were corrected according to Baars and Helling (1985).

Cohort analysis of *S. thompsoni* aggregates and solitaries was performed using finite mixture distribution (FMD) modelling, implemented through the R package mixdist (R Core Team, 2013). This method applied a combination of Expectation-Maximization and Newton-type algorithms to compute the best fit to the observed data from among a series of distribution types (Normal, Lognormal, Exponential and Gamma). Mixdist was allowed to apply constraints on model parameters (e.g., number of cohorts, mean cohort size) to prevent over parameterization (Macdonald and Pitcher, 1979). The

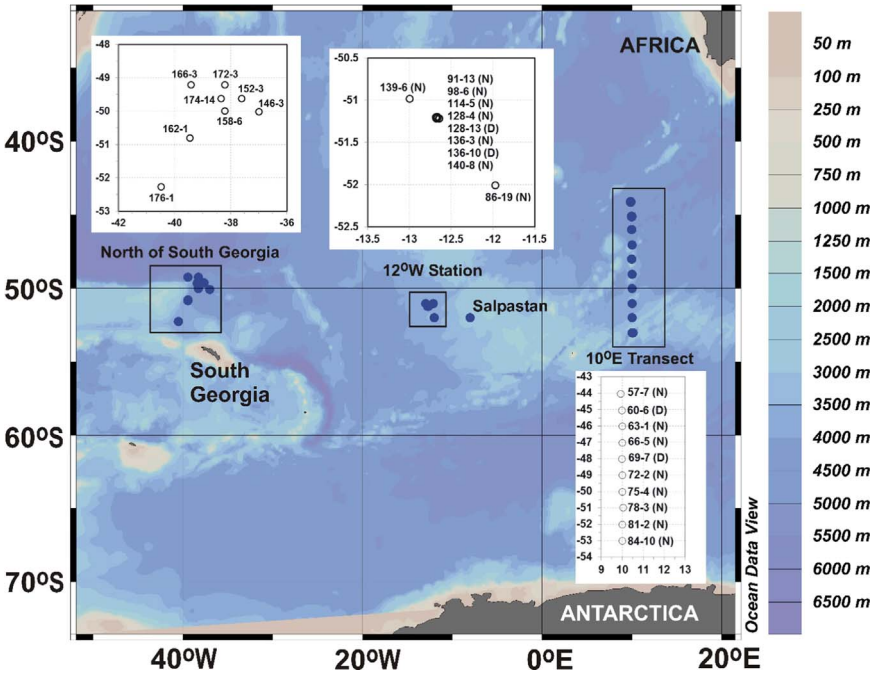

Fig. 1. Map of sampling locations in the Atlantic Sector of the Southern Ocean during January–March 2012 (ANT XXVIII/3).

identification of components was based on the appearance of distinct modal peaks in the size-frequency histograms. The number of measured individuals only allowed for reliably depicting the first 3–4 aggregate cohorts, which were subsequently used for growth estimates. Once identified, the means attributed to different cohorts were linked through time in a fashion thought to capture the growth trajectory of different, visually identified cohorts. The solitaries had low abundances and were combined into 5 mm size intervals, which allowed better visualization of major cohorts. Once identified, the same procedure as for aggregates was used to capture the growth trajectory of potential cohorts.

To compare salp length-density distributions among the major regions sampled, non-metric cluster analysis was performed in conjunction with the Bray-Curtis similarity index after log transformation [log10(x+1)] of salp abundance data in 2 mm (aggregates) and 5 mm (solitaries) size bins using the Plymouth Routines In Multivariate Ecological Research (PRIMER 6, Clarke and Warwick, 1994) computer package.

3. Results

3.1. Regional environments

While conducted in the proximity of the Antarctic Polar Front (APF), four main sampling locations covered a variety of hydrological environments (Strass et al., in this issue). With the exception of the 10°E transect however, majority of stations were conducted either at the APF or immediately south of it. Detailed description of the physical environment of investigated regions is presented in the paper by Strass et al. (in this issue) and summarized in Table 1.

In short, the 10°E transect was sampled between 44° and 53°S and crossed three major Southern Ocean frontal systems: the Subantarctic Front (SAF), APF and Southern ACC Front (SACCF). Stations along the transect were separated by the APF situated at ~49°S into 10°E north and 10°E south regions. The former region was characterized by the highest (7.95 °C) mean surface water temperatures and low (~0.4 mg m^{-3}) Chl-a concentrations, while the latter represented colder (3.6 °C) and more productive (~0.8 mg m^{-3}) waters south of the APF (Table 1). In the 10°E- north region, CTD profiles potentially identified a strong warm-core eddy situated between 45 and 46°S (Strass et al., in this issue). The Salpastan station (52°S-8°W) was conducted within the cold water meander representative of the Winter Water (Strass et al., in this issue) usually found south of the SACCF with both lowest mean water temperatures (1.9 °C) and Chl-a (~0.1 mg m^{-3}) (Table 1).

The region immediately west of the cold and unproductive meander (12°W), where the mesoscale grid survey and eulerian study were conducted, was representative of a large-scale phytoplankton bloom (mean Chl-a concentration of 1.65 mg m^{-3}) that may have lasted for several months and was possibly influenced by upstream high Chl-a areas through advection (Strass et al., in this issue). During the eulerian study, sediment traps were deployed that drifted minimally (see Iversen et al., in this issue), mean current speed was low (< 0.05 m s^{-1}) and environmental conditions were stable (Strass et al., in this issue). The above provided confidence that the eulerian sampling conducted between January 31 and February 17, 2012 was carried out in the same water mass and thus likely represented an observational time series for the same salp population. The environmental variables were characteristic of the APF zone and similar to 10°E south region (Table 1). Lastly, north of South Georgia in the Georgia Basin the meso-scale survey was carried out in the proximity of the SAF and APF (Strass et al., in this issue). This region was influenced by warm (mean 6.4 °C) and productive (mean ~1.3 mg m^{-3}) waters (Table 1) and was characterized by a strong eastward flowing meander (Strass et al., in this issue).

3.2. Salp density and distribution

Salps were sampled at all but one station (St. 162-1) throughout the study (Fig. 2). Three species of salps were identified including *Salpa thompsoni*, *Iasis zonaria* and *Pegea confoederata*. *S. thompsoni* was the only species collected south of the APF and it was present in all but two samples. *I. zonaria* and *P. confoederata* were only captured north of the APF along the 10°E north, where they accounted for up to 46 and 99% of salp abundance and biomass, respectively (Fig. 2). *P. confoederata* was only sampled at stations influenced by the warm-core eddy (Stns. 60-6 and 63-1) but was particularly prominent on St. 63-1 (Fig. 2; Strass et al., in this issue).

Salps are known to have patchy distribution and this was reflected

Table 1
Regional summary of environmental parameters and salp abundance and biomass in the Atlantic sector of the Southern Ocean (mean value ± 1SD). Stations along the 10°E transect were separated by the APF situated at ~49°S into 10°E north and 10°E south regions. Surface temperature, salinity and Chl-a were measured at ~ 5 m depth.

Region	Sampling period (2012)	Surface temperature (° C)	Surface salinity	Surface chlorophyll-a (mg m^{-3})	Salp abundance (ind.1000 m^{-3})	Salp contribution to total abundance (%)	Salp biomass (mg DW m^{-3})	Salp contribution to total biomass (%)
10°E north	Jan 11–15	7.95 ± 2.09	33.83 ± 0.38	0.39 ± 0.10	6.2 ± 7.7	2.3 ± 2.5	0.8 ± 1.4	18.7 ± 25.8
10°E south	Jan 16–22	3.60 ± 1.32	33.79 ± 0.03	0.75 ± 0.35	212.5 ± 121.8	67.6 ± 14.6	2.0 ± 1.4	37.5 ± 23.2
Salpastan	Jan 26	1.96	33.85	0.10	3149.5	96.6	20.5	93.5
12°W	Jan 31–Feb 17	3.72 ± 0.46	33.79 ± 0.04	1.65 ± 0.38	112.1 ± 58.5	23.6 ± 13.3	1.1 ± 1.0	16.5 ± 11.5
South Georgia	Feb 25–Mar 5	6.40 ± 1.21	33.69 ± 0.07	1.28 ± 0.58	520.1 ± 699.4	45.8 ± 29.5	6.2 ± 12.1	30.3 ± 33.2

in the high variability of the salp abundance, biomass and contribution to total macroplankton (Fig. 2). Overall, however, *S. thompsoni* contribution to total zooplankton was generally << 40% in terms of both abundance and biomass. Exceptions were two stations, namely Salpastan and 146-3, where > 95% of the RMT-8 catch comprised *S. thompsoni*. In addition, stations in the vicinity of the APF (e.g. Stns. 72-1 and 75-4 or 166-3 and 172-1) had elevated (> 30%) contribution of salps (Fig. 2). The lowest mean *S. thompsoni* abundance and biomass were observed north of the APF, and the highest at the Salpastan station (Table 1). The remaining three regions, 10°E south, 10°W and South Georgia, had intermediate and variable salp densities (Table 1, Fig. 2).

3.3. Regional salp biology

The average size distribution of *S. thompsoni* aggregates was similar in the 10°E south and South Georgia basin regions (Fig. 3). Although the bulk of the distribution was always concentrated on the left, with small aggregates (6–10 mm) dominating, the overall salp size distributions were strongly right-tailed (Fig. 3). In the 12°W region, while distribution was skewed to the right, small aggregates appeared to be the most numerous size group (Fig. 3). Both the 10°E north and Salpastan regions displayed multi-modal size distributions with modes at 10–12, 18 and 26 mm (Fig. 3). In the 10°E north region, aggregates with a mode of 10 mm dominated samples, while at Salpastan aggregates with a mode of 18 mm were most numerous, followed by aggregates with a mode of 12 mm (Fig. 3). The cluster analysis showed that all regions, except north of APF, had highly similar (≥50% similarity) size distributions (Fig. 4).

Size distributions of *S. thompsoni* solitaries were most similar between 10°E south, 12°W and South Georgia Basin, while Salpastan and 10°E north clustered independently (Fig. 4). The between regions common features in solitaries were (a) multi-modal size distributions and (b) a substantial proportion of small (< 50 mm and even < 30 mm) individuals (Fig. 5). At Salpastan and the South Georgia Basin very small solitaries (< 10 mm) were present in samples, while the smallest solitaries recorded in the 10°E south and 12°W regions were 18–20 mm in length. At 10°E north solitaries smaller than 35 mm were not sampled (Fig. 5).

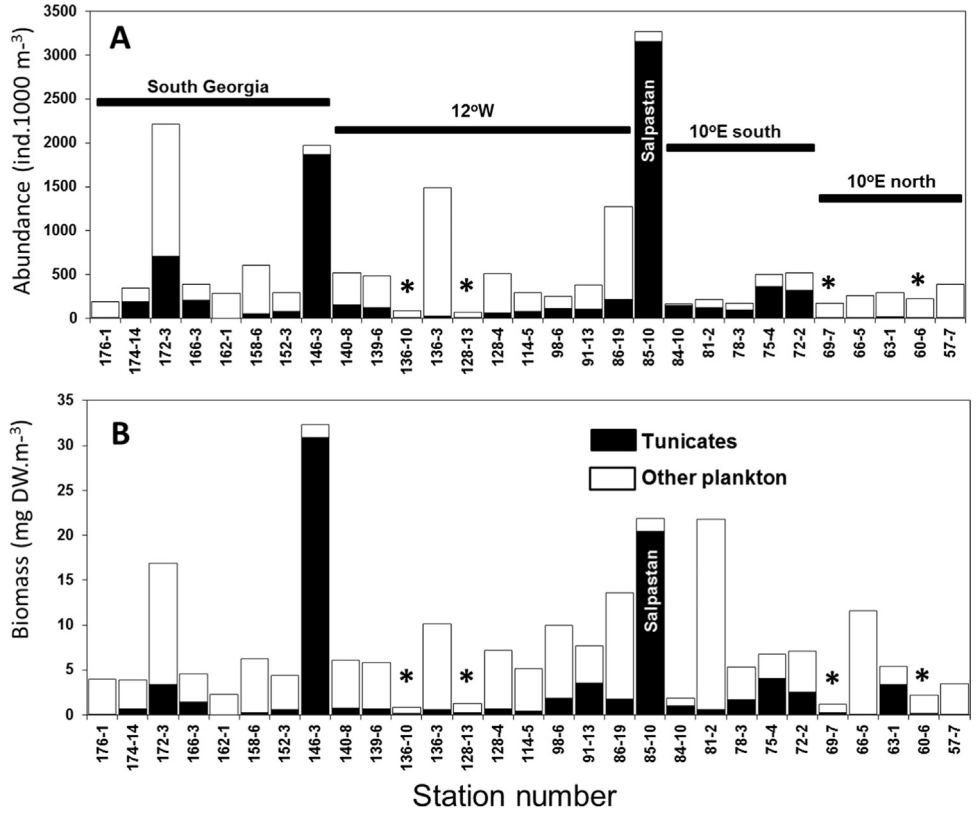

Fig. 2. Abundance (ind.1000 m^{-3}) and biomass (mg DW m^{-3}) of pelagic tunicates and total macrozooplankton from RMT-8 samples in the Atlantic Sector of the Southern Ocean during January–March 2012. Asterisks show stations that were conducted during daytime.

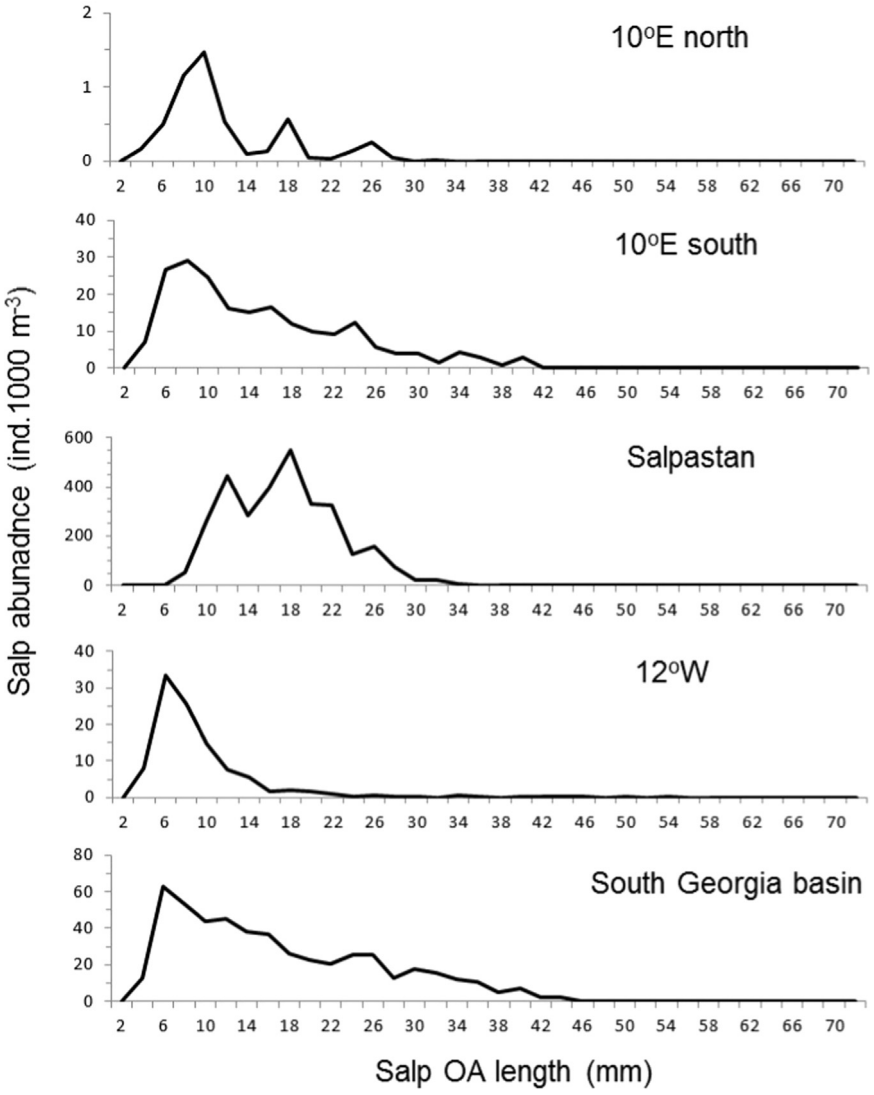

Fig. 3. Size (mm) distributions of *Salpa thompsoni* aggregates averaged for five major sampling regions during January–March 2012 in the Atlantic Sector of the Southern Ocean.

The aggregate to solitary (A/S) ratio was lowest at the 12°W region and highest at the 10°E south region (Fig. 6). There was a general trend of decreasing A/S ratios from east to west (Fig. 6). Overall, the full set of aggregate stages were present in all regions but their proportions were different (Fig. 6). In the 10°E north region, early (stage 1) and spawned females (stage 5) were prevalent. In addition, functional aggregate males contributed ~12% to the total aggregate population (Fig. 6). Although many spawned aggregates were present, no recently released solitary embryos were found in RMT-8 samples. However, a few small solitaries (embryos) were observed in the RMT-1 samples (Pakhomov E.A, unpublished data). Solitaries were dominated by 4B to 5B stages suggesting resent chain releases in the region (Fig. 6). At the 10°E south, the aggregates were clearly dominated by stages 0 to 2 which again was reflected in the substantial proportion of solitaries that had recently released chains (Fig. 6). Spawned females accounted for ~10% of aggregates and early stages (2–3) dominated among solitaries (Fig. 6).

Salpastan aggregates had an advanced stage composition with spawned females dominating. These were followed by the aggregate stages 2 to 4 and conformed well with freshly released embryos (solitary stage 0) that accounted for nearly 80% of all solitaries sampled (Fig. 6). During the eulerian study (12°W region) and in the South Georgia Basin the aggregate stage composition was highly skewed towards early (0–2) stages that comprised ~83–88% individuals (Fig. 6). In both regions, solitaries were characterized by developing and chain releasing individuals with slightly more advanced solitary development composition in the 12°W region (Fig. 6).

3.4. Eulerian study

During the eulerian study, the size distribution of aggregates and solitaries was consistent over time except at St. 136 conducted on February 14th (Figs. 7 and 8). Although a small number of large (> 30 mm) aggregates was consistently sampled, over 90% of all aggregates were smaller than 20 mm (Fig. 7). Similarly, at the majority of stations 25–100 mm solitaries dominated catches (Fig. 8). At St. 136 most of the aggregates ranged in length between 12 and 22 mm and solitaries had two major peaks at 97 and 117 mm (Figs. 7 and 8).

It was not surprising that aggregate developmental composition was clearly dominated by stages 0–1 throughout the eulerian study and showed only slight stage progression over the period of observation (Fig. 9). The solitary stage composition was variable and, with the exception of St. 136, usually had a full suite of stages from 2–5B. It is noteworthy that on Jan 31st, Feb 4th, 9th, 14th, 15th and possibly 17th the chain released, or ready to be released, solitaries (4B and 5B combined) contributed 10 to 71% to total solitary counts (Fig. 9). This suggests that chain-releasing events may have occurred just prior to sampling or happening very soon. It was also apparent in the

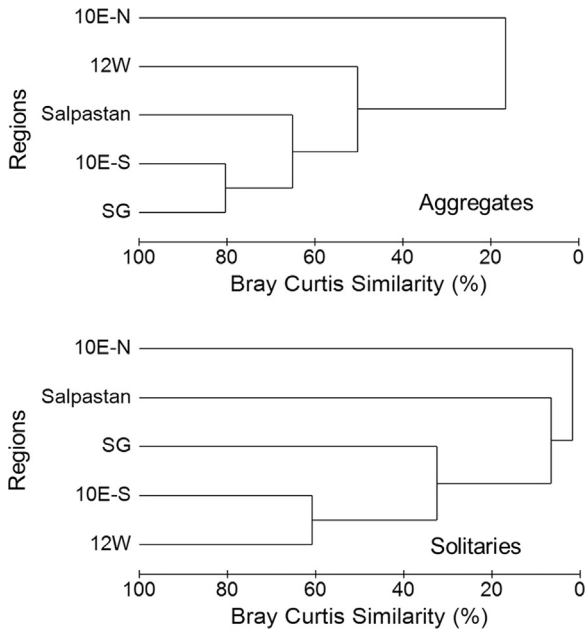

Fig. 4. Similarities in the size distribution of *Salpa thompsoni* aggregates and solitaries in five major regions of the Atlantic Sector of the Southern Ocean during January–March 2012.

appearance of aggregates at stages 0 and 1 (Fig. 9). The A/S ratios, with the exception of St. 136, varied between 10 and 50 and overall increased towards the end of the study (Fig. 9).

Cohort analysis of daily aggregate samples usually identified three (range 2–4) clear cohorts. When plotted by day, we were able to follow and parameterize five linear patterns (Fig. 10A). It was assumed that each pattern represented a growth trajectory of an individual cohort and in this study an increase in size of synchronously released aggregate blocks. Size of the buds in the block usually increases with the solitary form maturation. Usually, they are ready for release at ~3–5 mm size and aggregates are ready to release embryos on average by 25 mm OA length (Foxton, 1966; Von Harbou, 2009). Using regressions obtained for individual cohorts (Fig. 10A), the duration of salp growth from 4 to 25 mm was estimated to range between as short as 27 and as long as 60 days, with a mean of 43.8 ± 14.5 days (Fig. 10A). Growth rates estimated from change in body length over time ranged from −0.2 to 1.6 mm day^{-1} with a mean of 0.62 ± 0.53 mm day^{-1}. Maximum daily growth rates expressed as percentage of body length (BL) reached 18.6% but on average were 6.3 ± 5.2% per day (Fig. 10A). Calculated (using regressions) mean growth rate was 0.53 ± 0.18 (range 0.4–0.8) mm day^{-1} or 5.7 ± 1.5% (range 3.7–9.1) BL per day which showed decrease with the salp length (Fig. 10B).

Cohort analysis of daily solitary catches identified between 3 and 7 individual cohorts. When plotted, up to 6 linear patterns of sequential cohorts were traceable (Fig. 11A). We assumed that each pattern represented a growth trajectory of a distinct cohort, reflecting synchronously released young solitaries by female aggregates. Literature sources suggest that young solitaries are released as ~ 4 mm long individuals, while solitaries are ready to liberate their first block of aggregates by 55 (range 45–80 mm) or 70 mm (range 51–89 mm) according to Foxton (1966) and Von Harbou (2009), respectively. Using regressions obtained for individual cohorts (Fig. 11A) the duration of solitary salp growth from 4 to 55 mm or to 70 mm would range from 16 to 23 days with mean of 20 ± 3 days, or from 20 to 30 days with mean of 25 ± 3.6 days (Fig. 11A). Calculated (using regressions) mean solitary growth rate was 2.83 ± 0.42 (range 2.2–3.3) mm day^{-1} or 5.3 ± 3.6% (range 1.8–20.7) BL per day. The latter was highest in 10–15 mm solitaries, sharply decreasing with salp length reaching < 2% in specimens of ~ 120 mm (Fig. 11B).

3.5. Gut pigment dynamics

Plotted separately for aggregates and solitaries, gut pigment content of salps increased with the salp length and the relationship was best approximated by a power function (Fig. 12). For both forms, gut pigment content was substantially lower at the Salpastan station. It appears that aggregate gut pigment values were indistinguishable between 12°W and South Georgia Basin (Fig. 12). Although slopes were very similar, gut pigment contents of solitaries were on average consistently ~ 3 fold higher at the 12°W region compared to the South Georgia Basin (Fig. 12).

There was no significant relationship between salp abundance, biomass or percentage contribution to total macroplankton and seawater temperature and salinity, which always explained < 5% of salp density variability (data not shown, p in all cases > 0.1). Chlorophyll-a concentrations explained ~42% of salp density variation, although this relationship was not significant (Fig. 13). This negative relationship was indeed largely driven by a single observation of high salp abundance at the low Chl-a Salpastan station.

4. Discussion

4.1. Spatio-temporal differences in Salpa thompsoni biology

Seasonally, the sampling window of this study coincided with the mid Austral summer to the beginning of fall period and overall lasted 54 days. With the exception of the Salpastan location, most of the aggregates were small, ranging in size between 5 and 10 mm (Fig. 3). This is not unusual, as according to Foxton (1966) the size cohort 5–10 mm numerically dominates samples, accounting for 40–90% of sampled aggregates with a characteristic right tailed distribution, from August to April (Fig. 26 in Foxton, 1966). It is also noticeable that a substantial number of aggregates larger than 25–30 mm (potentially functional aggregate males) were consistently sampled between September and February and were absent during Austral winter, April to August (Fig. 26 in Foxton, 1966). It should be pointed out that in Foxton's study aggregates were sampled across their circum-Antarctic range, in various sectors (and in different years) of the Southern Ocean including the western (30-50°W) Atlantic during March, August, October and November; the eastern (0-20°E) Atlantic during January-April, June, July, September and October; the Indian sector in May, November and December; and finally in the Pacific during September (Foxton, 1966). Indeed, multi-year and multi-sector sampling may have contributed to the high similarity in aggregate lengths distributions. There are two important observations that can be drawn from the Discovery data. First, the size distribution of aggregates may be either similar (e.g., November) or dramatically different (e.g., September, October and January) in a particular month depending on the sector and year of sampling (Fig. 26, and Table 14 in Foxton, 1966). Second, during the winter months, specimens within the size range 10–20 mm dominated aggregates, and this was postulated to imply very slow growth rates (Foxton, 1966). The prevalence of small aggregates during the summer months is deemed to be a clear indication of active asexual reproduction, which is confirmed by the size and stage composition dynamics of solitaries in Foxton (1966). A similar demographic composition has been observed in various sectors of the Southern Ocean (e.g. Chiba et al., 1998; 1999; Pakhomov et al., 2006; 2010; 2011; Ono et al., 2010; Ono and Moteki, 2016). The persistence of a similar size dynamic across spring to fall is however puzzling and points to continuous reproduction for nearly 8 months, resulting in several (annual) cohorts developing during this period. The absence of high resolution time series however precludes any definitive cohort identification.

In our study, all samples were collected across the Atlantic Sector of the Southern Ocean over a two month period. Nevertheless, the most spatially (separated by 50° of longitude) and temporally separated (41

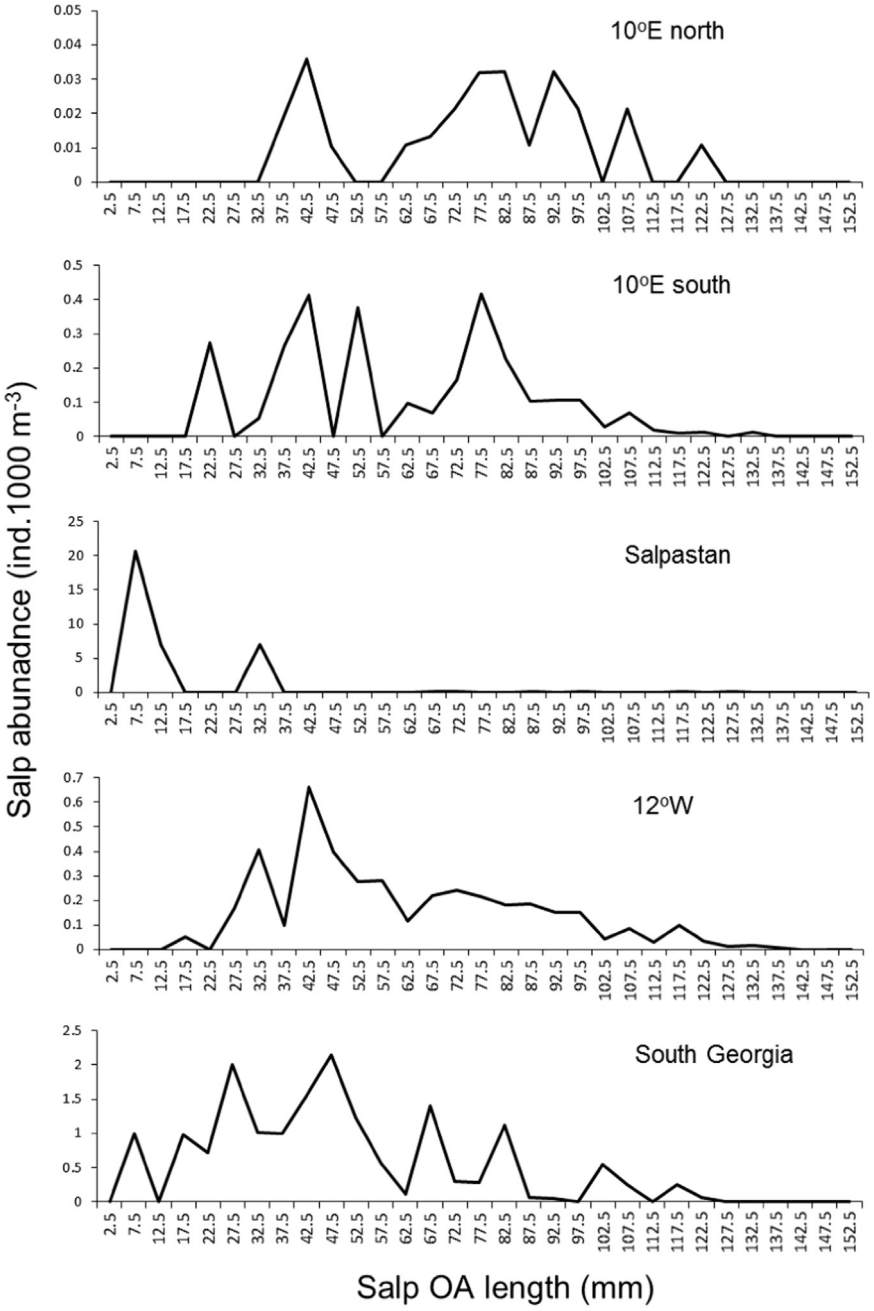

Fig. 5. Size (mm) distributions of *Salpa thompsoni* solitaries averaged for five major sampling regions during January–March 2012 in the Atlantic Sector of the Southern Ocean.

days) regions, the 10°E south stations and the South Georgia Basin, had remarkably similar *S. thompsoni* population demographics (Figs. 3–6). On the other hand, the most dissimilar *S. thompsoni* population compositions were encountered only few days and ~ 4° longitude apart, at the Salpastan and 12°W locations (Figs. 1 and 4). Salpastan was conducted in a large, low temperature and low Chl-a ACC meander that persisted in the area for some time (Strass et al., in this issue). The Salpastan aggregates were in highly advanced developmental stages with the majority having already liberated embryos. This was confirmed by the predominance of freshly released solitaries (stage 0) in the samples (Fig. 6). High salp and low Chl-a concentrations may have been the result of salps controlling phytoplankton development in this water mass (Fig. 13), which in turn may have halted development and continuous reproduction of *S. thompsoni* in this region. It is noteworthy that salps numerically and volumetrically dominated the macroplankton community, with other groups being extremely scarce in this region (Fig. 2). Foxton (1966) proposed that there may be a significant predation on freshly released embryo solitaries that results in a remarkable discrepancy between the theoretical embryo production predicted from the number of aggregates with developed embryos and the number actually sampled in the water column. In the Salpastan region, low predation pressure may have explained the prominence of the young solitaries in the samples. Indeed, in all other regions yearly solitaries (stage 0) were generally absent in the RMT-8 samples despite the presence of spawned aggregates. Unlike Salpastan, in the other regions macroplankton and micronekton samples were dominated by predatory amphipods (*Themisto gaudichaudii*), euphausiids (*Euphausia triacantha*) and myctophids, which are shown to consume small salps (Hunt et al., 2013; Kruse et al., 2015).

Several important conclusions can be drawn from our study. First, it appears that *S. thompsoni* development is not strongly constrained

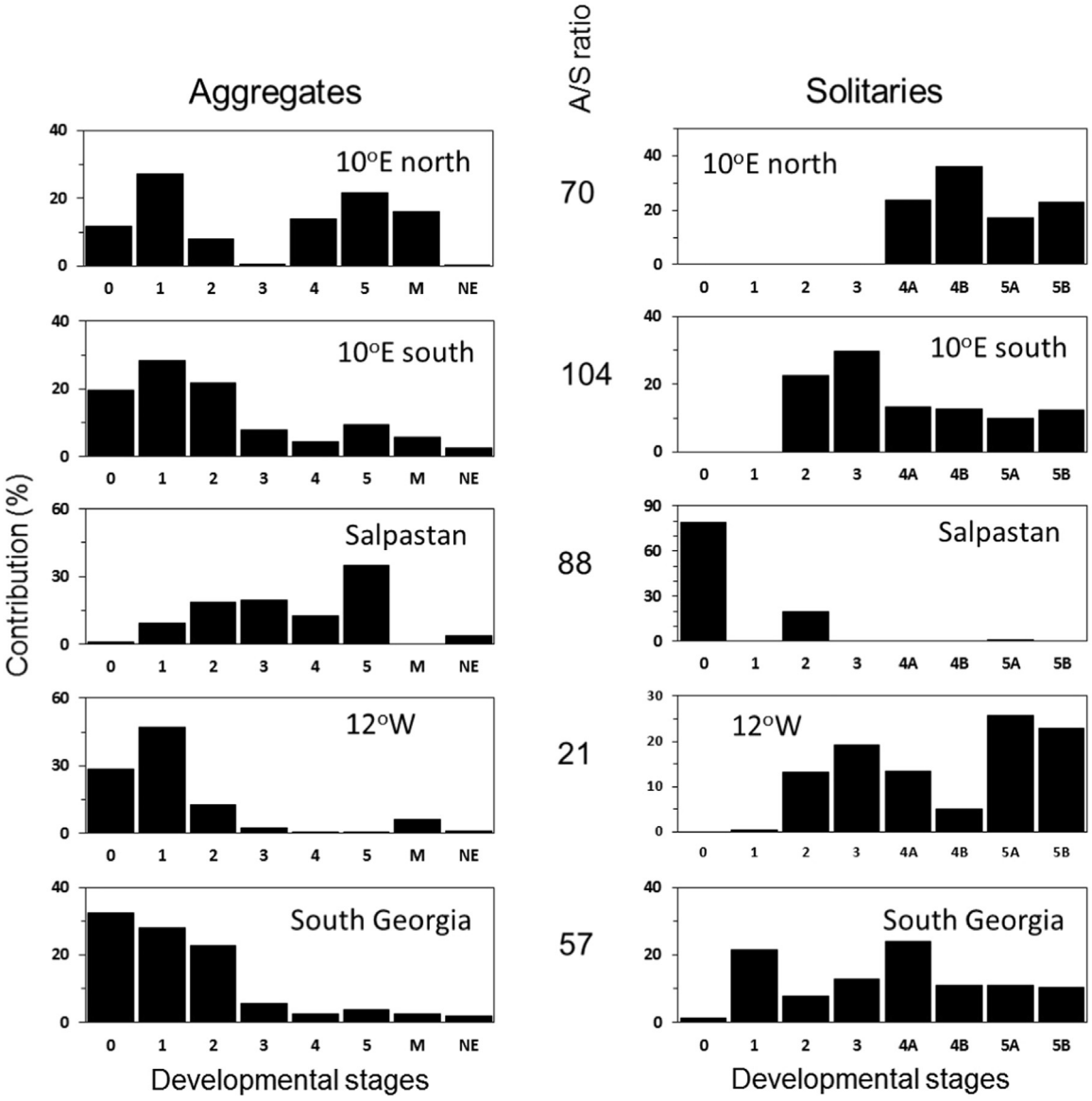

Fig. 6. Developmental stage composition of aggregates and solitaries and well as aggregate/solitary (A/S) ratios in five major sampling regions of the Atlantic Sector of the Southern Ocean during January–March 2012.

by either longitude or season, and assumes similar population demographics spatio-temporally, at least within the Atlantic sector of the Southern Ocean but likely also beyond it. Second, the Salpastan exception may suggest environmental (e.g., Chl-a levels, low water temperatures) or predator thresholds, which either independently or synergistically allow salps to either control (Salpastan) or not (other regions) the phytoplankton bloom development in the water masses near the APF. Third, in regions with high Chl-a concentrations (> 1 mg m^{-3}) *S. thompsoni* may continuously reproduce for months and thus may not be restricted to a single sexual and asexual reproduction cycles. The latter is hard to prove as it requires seasonal sampling of the same population and such observations do not exist in the Southern Ocean. Nevertheless, in the fall survey of the Bellingshausen Sea, it was preliminarily calculated that two clear cohorts of aggregates may have been spawn roughly 35–40 days apart (see below, Pakhomov et al., 2006). Overall, the general similarity in the *S. thompsoni* population dynamics (and dissimilarities for that matter) should be a product of the initial regional conditions existing before the salp development begins. This urgently requires further attention in order to re-evaluate the *S. thompsoni* life cycle. In this regard, the recent explosion of the research of the *S. thompsoni* ecology in the high Antarctic regions representing marginal species tolerance conditions (e.g. Chiba et al., 1999; Pakhomov et al., 2006; 2010; 2011; Ono and Moteki, 2013, 2016; Ono et al., 2010) is critical to understand how salp life cycle may change after encountering unfavorable environments during its expansion southward (Pakhomov et al., 2002). Currently, we know little about *S. thompsoni* growth and developmental rates at its main habitat, the Antarctic Polar Frontal Zone, and how it may be affected by low temperature and Chl-a conditions. In this regard, the most powerful observations in our study were made at the 12°W during the eulerian study, which will be discussed in detail below.

4.2. Salpa thompsoni *growth rates*

Salp growth rates are summarized by Madin and Diebel (1998), showing the remarkable growth potential of pelagic tunicates. Recalculated values indicate that cold temperate species (water temperature 11–15 °C) may grow 0.7–10.1 mm daily, which could account for 10–41% BL per day in small individuals and 5–14% BL per day for larger aggregates and solitaries (Madin and Diebel, 1998). In the case of warm temperate species (18–25 °C), daily growth rates of 10–15 mm day^{-1} (94–120% BL day^{-1}) and 3–4 mm day^{-1} (2–5%

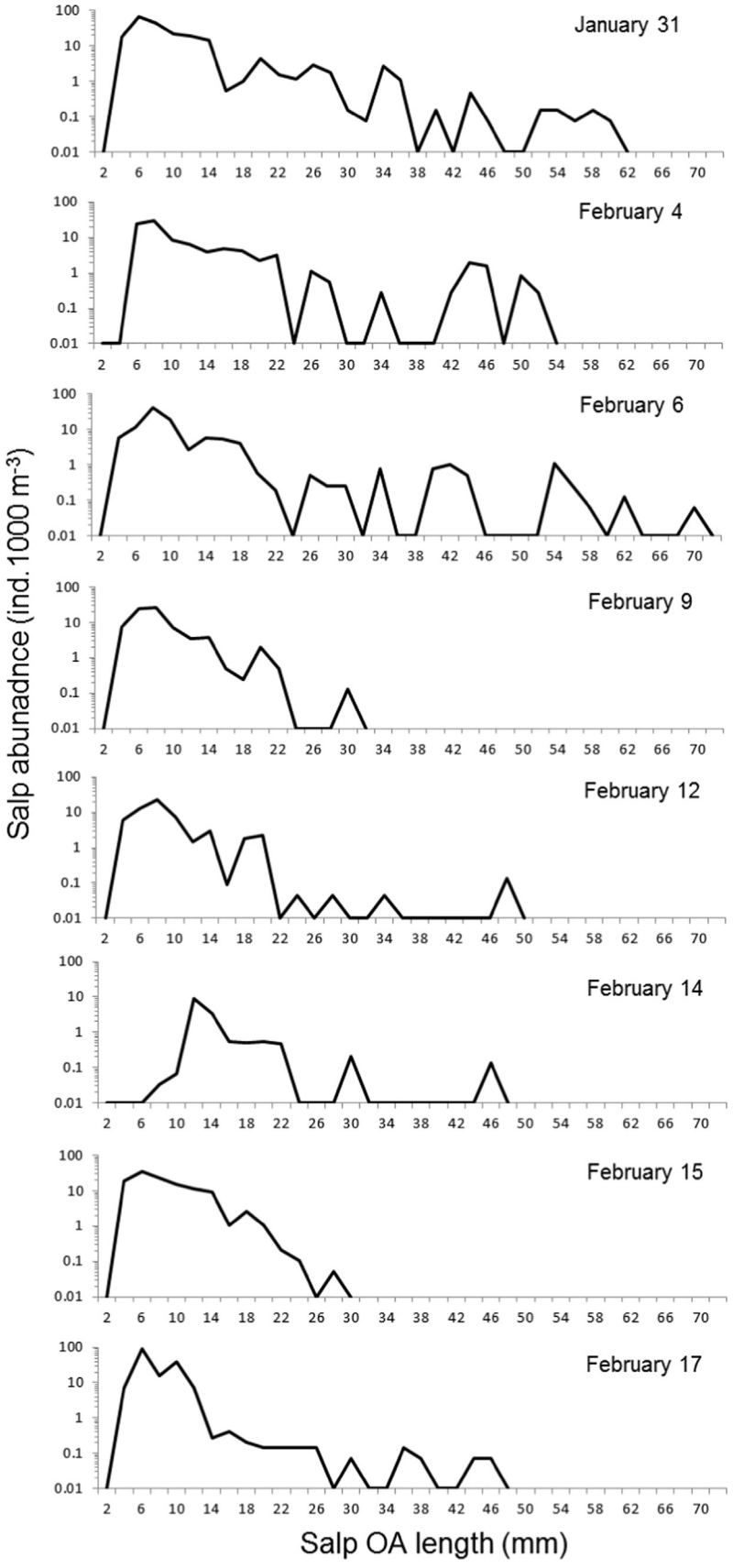

Fig. 7. Size distributions of *Salpa thompsoni* aggregates (log abundance) during the eulerian study at 12°W between January 31 and February 17, 2012.

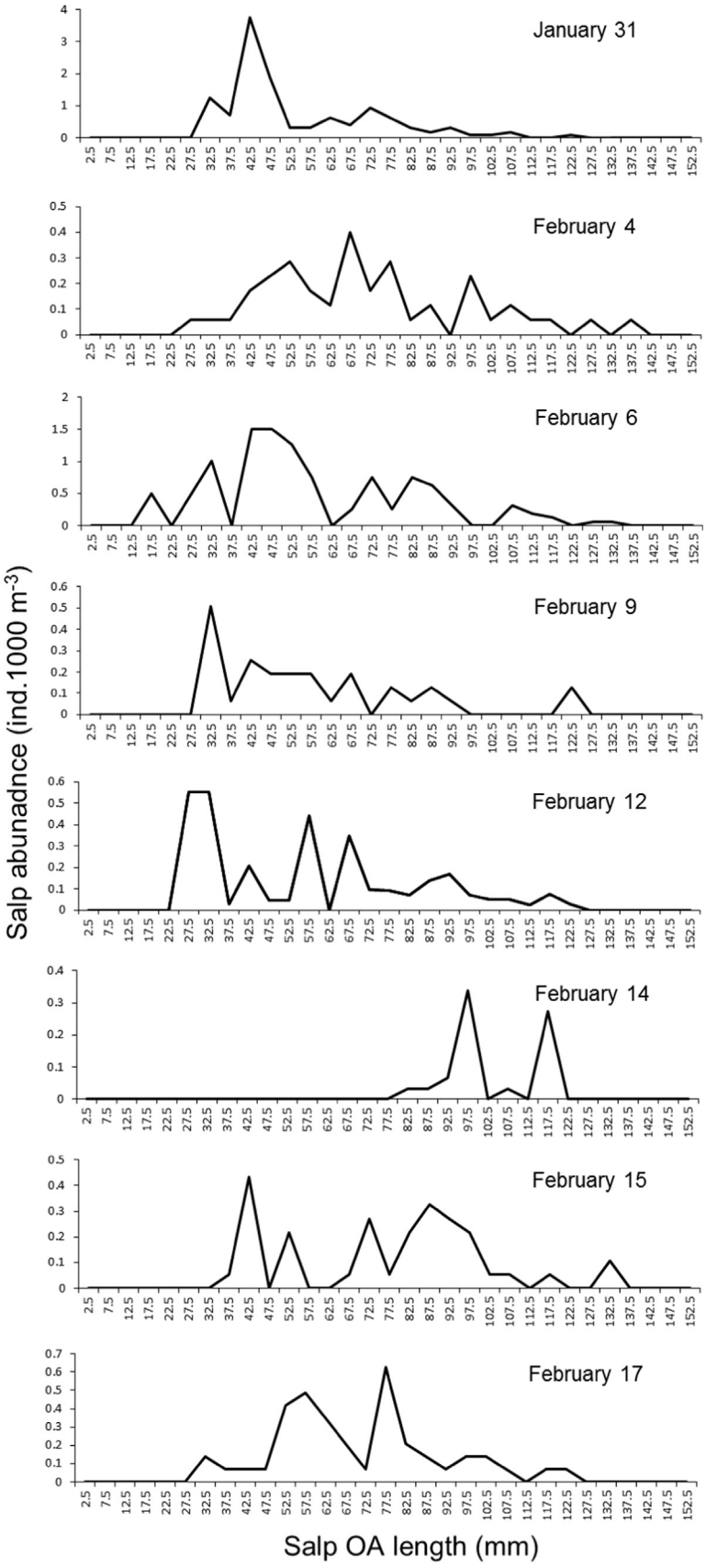

Fig. 8. Size distributions of *Salpa thompsoni* solitaries during the eulerian study at 12°W between January 31 and February 17, 2012.

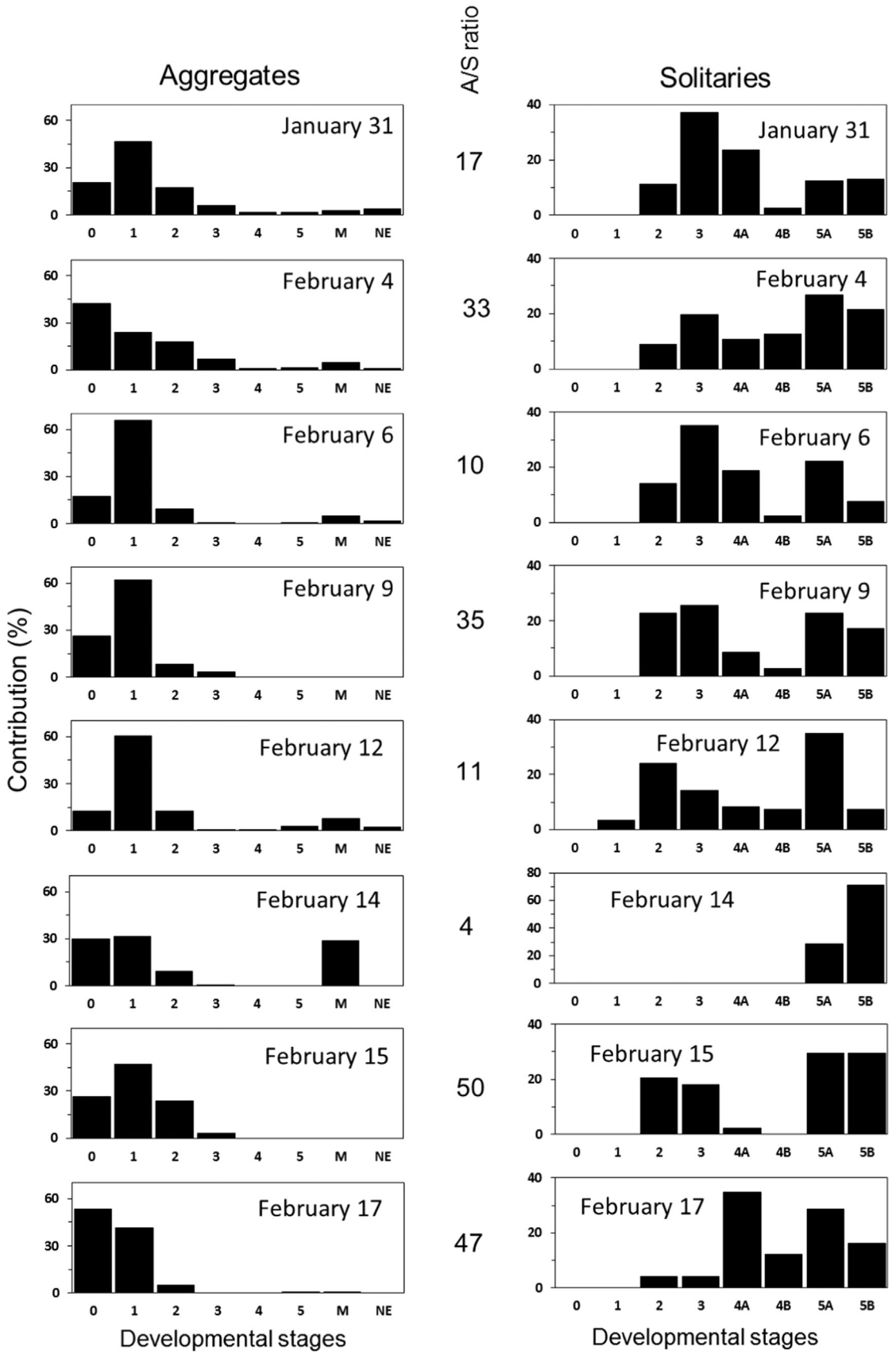

Fig. 9. Developmental stage composition of aggregates and solitaries and well as aggregate/solitary (A/S) ratios during the eulerian study at 12°W between January 31 and February 17, 2012.

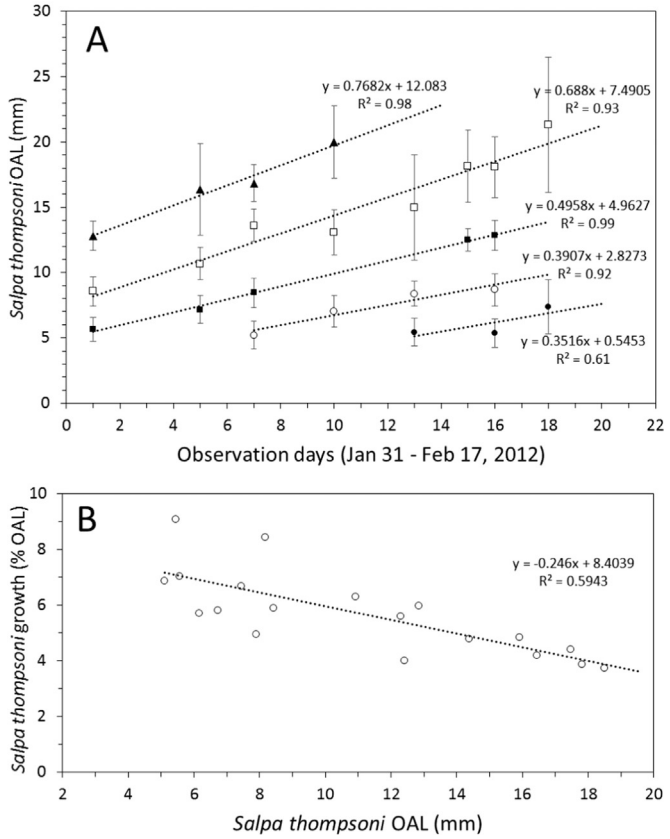

Fig. 10. Growth trajectories of individual cohorts of *Salpa thompsoni* aggregates (A) and their mean relative growth rates (B) during the eulerian study at 12°W between January 31 and February 17, 2012. Error bars show one standard deviation.

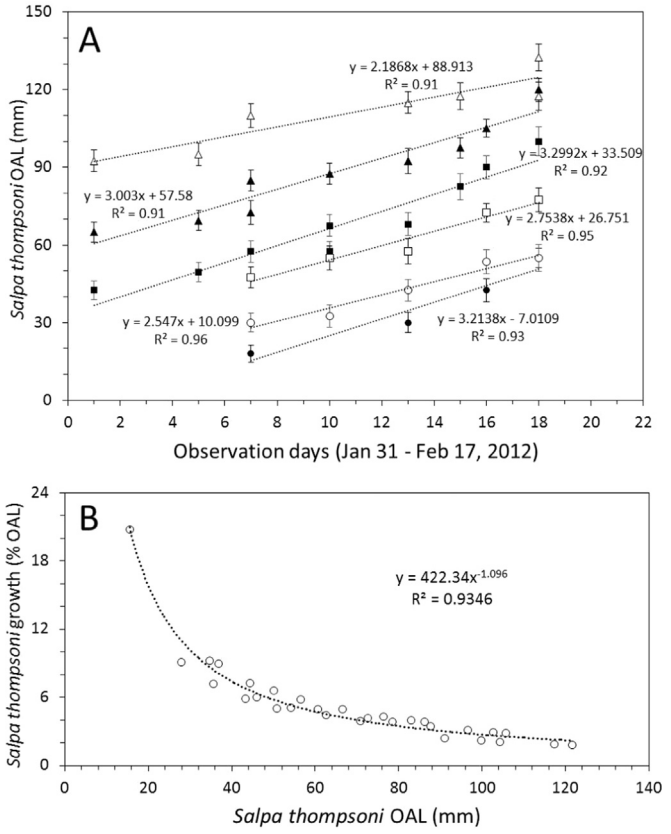

Fig. 11. Growth trajectories of individual cohorts of *Salpa thompsoni* solitaries (A) and their mean relative growth rates (B) during the eulerian study at 12°W between January 31 and February 17, 2012. Error bars show one standard deviation.

BL day^{-1}) are reported for small and large individuals, respectively (Madin and Diebel, 1998). Small tropical species, such as *Thalia democratica*, can grow as fast as 20–28% BL h^{-1} in favorable conditions (Heron, 1972; Madin and Diebel, 1998).

Currently, there is only one study estimating *S. thompsoni* growth rates in the natural environment (Loeb and Santora, 2012). Using cohort analyses of repeated sampling, these authors calculated that growth rates of aggregates and solitaries were on average 0.4 ± 0.05 and 0.23 ± 0.04 mm day^{-1}, respectively (Loeb and Santora, 2012). It appears that aggregates can grow as fast as 4% BL day^{-1} at 10 mm OAL and as slow as 1.3% BL day^{-1} at 30 mm OAL. Solitaries grew much slower, e.g. 4.6% and 0.3% BL day^{-1} at lengths of 5 and 70 mm OAL, respectively. Thus, from the moment of release, aggregates can grow to 25 mm in ~ 55 days and solitaries would take another ~220 days to grow to 55 mm length (~280 days to 70 mm). Accordingly the entire *S. thompsoni* life cycle would take 9 to 12 months to complete, in a good agreement with the life cycle suggested by Foxton (1966) (Loeb and Santora, 2012). However, this life cycle does not explain the peculiar *S. thompsoni* demographics, specifically the prevalence of small aggregate, in the Southern Ocean during spring to fall.

There are two unpublished *S. thompsoni* growth rate estimates. First can be inferred from the study in the Bellingshausen Sea when observations were carried out 12 days apart during austral fall at surface water temperatures of < 0 °C (Pakhomov et al., 2006). Two cohorts were identified, 13 and 30 mm aggregates with estimated mean growth rates of 0.41 (or 3.25 BL day^{-1}) and 0.36 mm day^{-1} (or 1.2% BL day^{-1}), respectively. Assuming linear growth rates, these two cohorts would have been separated by 35–40 days. Second, preliminary data collected in the proximity of the APF during late summer (Von Harbou, 2009) showed that 10–30 mm (OAL) aggregates grew 0.6–0.9 mm day^{-1} at stations with Chl-a < 1 mg m^{-3} and about 0.9–1.4 mm day^{-1} at stations with Chl-a > 1 mg m^{-3}. This was roughly equivalent to 6–9% BL day^{-1} in the low Chl-a region for ~ 10 mm OA length aggregates and 2–3% BL day^{-1} for ~ 30 mm OA length aggregates. In the high Chl-a region, growth rates were ~ 9% BL day^{-1} for ~ 10 mm OA length aggregate and 4.7% BL day^{-1} for ~ 30 mm OA length aggregate. Given the growth rates above, in the cold shelf environment of the Bellingshausen Sea aggregates can reach a size of 25 mm in roughly 58 days, while in the APF region this may take as little as 15–23 and 23–35 days in the low and high Chl-a environments, respectively. It was interesting to note that the embryo size was ~ 17% smaller in the region of high (> 1 mg m^{-3}) Chl-a concentrations compared to regions with low (< 1 mg m^{-3}) Chl-a concentrations (Von Harbou, 2009). While this is counterintuitive, it was previously shown that in the high Chl-a environments *S. thompsoni* feeding (and thus reproductive investment) can be impaired due to high particle concentrations (Perissinotto and Pakhomov, 1997, 1998). However, it appears that it may potentially be compensated by higher growth rates of aggregates at high Chl-a habitats.

The growth rates measured for both aggregate and solitary forms in our eulerian study were comparable to the Von Harbou (2009) study but generally were 2–3 fold higher than previously estimated for *S. thompsoni* in Pakhomov et al. (2006) and by Loeb and Santora (2012). They were also comparable to the lower range of the cold temperate salp species in other regions of the World Ocean (Madin and Diebel, 1998). The growth rates estimated obtained in our eulerian study indicate that *S. thompsoni* may complete its entire life cycle (sexual+asexual components) in 64–69 and 83–90 days if solitaries mature on average at 55 mm or 70 mm OAL, respectively. This is substantially shorter that previously proposed (Foxton, 1966; Loeb and Santora, 2012). The findings of our eulerian study suggest that mature solitaries may release blocks of aggregates as often as every 6 days. It was also remarkable that small *S. thompsoni* solitaries may grow rapidly (> 20% BL day^{-1}), which is the range of the lower end of the published rates for temperate salp species (Madin and Diebel, 1998).

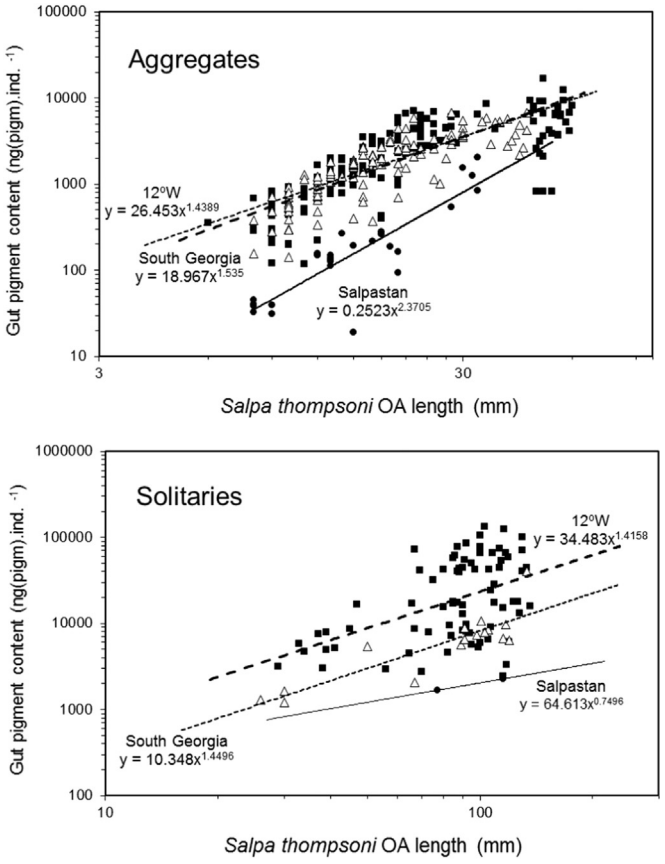

Fig. 12. Gut pigment contents of *Salpa thompsoni* aggregates (A) and solitaries (B) in Salpastan (solid black circles), 12°W (solid black square) and South Georgia Basin (open triangles) regions, January–March 2012. Regression lines are best-fit power regressions.

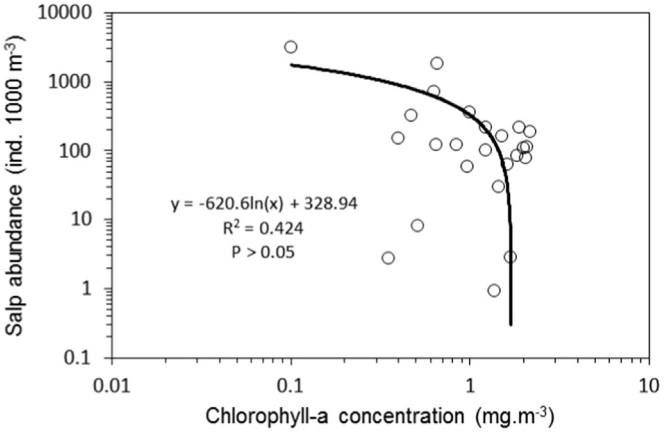

Fig. 13. Relationship between *Salpa thompsoni* abundance and surface chlorophyll-a concentration in the Atlantic Sector of the Southern Ocean during January–March 2012.

For comparison, mesocosm observations of the closely related temperate species *Salpa fusiformis* have revealed a very short life cycle at temperatures ~ 15 °C. Cultured solitaries rapidly grew their stolon and were ready to release their first chain of up to 150 aggregates on the sixth day (!) after leaving the maternal aggregate (Braconnot et al., 1988). The solitary form was able to produce up to 5 chains as often as every two days, and the released aggregates were able to grow to maturity in 12 days, allowing this species to complete its entire life cycle, including sexual and asexual reproduction, in only 18 days (Braconnot et al., 1988). Indeed, the small tropical-temperate species *Thalia democratica* was shown to complete its life cycle in 2–3 days under favorable conditions (Heron, 1972; Henschke et al., 2011).

In summary, it appears that both sexual and asexual reproduction of *S. thompsoni* (from egg to egg) may be completed within a 3-month period in the region of the APF zone implying more than one full life cycle during one calendar year in this area. This urgently requires further investigation because it may have significant implications for the magnitude of basin-scale carbon flux in the Southern Ocean (Pakhomov et al., 2002; Iversen et al., in this issue). The important finding of our study is a confirmation of potentially fast growth of solitary forms, particularly at the young stage. It is not only in line with previous measurements for other salp species but critical ecologically as recently released solitaries (as well as aggregates) are most vulnerable to active predation (Foxton, 1966; Kruse et al., 2015). It also explains the salp explosive development ("salp bloom phenomenon") under favorable environmental conditions.

One still unresolved issue in the *S. thompsoni* life cycle is the appearance, persistence and dynamics of male aggregates. The female aggregate chain has to be fertilized by a functional male (Godeaux et al., 1998) and our calculations indicate that first males may appear only after about 30–50 days of the aggregate chain release. Unfertilized eggs (up to 100%) inside *S. thompsoni* aggregates have been observed at the high Antarctic sampling locations in several studies (e.g. Chiba et al., 1998; 1999; Pakhomov et al., 2006; 2010; Ono and Moteki, 2016). It was speculated to be linked to the cold environments as well as to low salp densities and consequently low probability of functional males being present in the sampling region. However, the male conundrum in the *S. thompsoni* life cycle is not clearly resolved yet and urgently requires further work.

4.3. Distribution and feeding ecology

S. thompsoni densities encountered in our trans-Atlantic study, are well within the range previously reported in the Southern Ocean (e.g. Pakhomov et al., 2002). Except two stations, where tunicates clearly dominated, salps generally accounted for the modest to low proportion of macrozooplankton (Voronina et al., 1994; Voronina, 1998; Pakhomov et al., 2002). Chl-a and water temperature appeared to be poor predictors of salp abundance during our surveys, although suggested to be important in previous studies (e.g. Pakhomov et al., 2002; 2011). Nevertheless, > 40% of salp abundance could potentially be explained by Chl-a concentrations. In the Lazarev Sea, a strong negative relationship between salp density and Chl-a levels during the onset and development of the phytoplankton bloom has been documented (Perissinotto and Pakhomov, 1998). This was preliminary explained by the potential clogging of the filtering net of *S. thompsoni* at high particle concentrations (Perissinotto and Pakhomov, 1997; 1998). There was however no reliable relationship between salp densities and Chl-a concentrations prior of the phytoplankton bloom in the same region (Perissinotto and Pakhomov, 1998). It is thus possible that the combination of environmental factors prior to the onset of *S. thompsoni* active reproduction is critically important and ultimately may define whether salp population development is continuous or intermittent and whether salps will be able to control primary production and phytoplankton standing stock in the region (Madin and Diebel, 1998; Pakhomov et al., 2002). Indeed, examples of the potential effects of environmental history on *S. thompsoni* dynamics can be found north off Adelie Land (Chiba et al., 1998), in the Bellingshausen Sea (Pakhomov et al., 2006) and the Lazarev Sea (Perissinotto and Pakhomov, 1998; Pakhomov et al., 2011; Von Harbou, 2009).

In general, gut pigment contents of *S. thompsoni* aggregates and solitaries collected in different seasons and regions are comparable (Pakhomov et al., 2002; 2006; Pakhomov, 2004; Von Harbou et al., 2011). It was proposed that the phenomenon of similar gut pigment contents may be explained by the gut capacity. Salps are very efficient filtrators and are able to fill up their stomach in a matter of tens of minutes to a few hours (Von Harbou et al., 2011). Since gut passage

time in salps is size and likely temperature dependent, and generally amounts to several hours (Pakhomov et al., 2002), all salps may have similar amount of pigments in their stomachs in a wide range of surface Chl-a levels. Nevertheless, ~ 60% of the variation in individual salp gut contents may be explained by salp body size and ambient Chl-a concentrations (Pakhomov et al., 2002; Von Harbou et al., 2011). Although pigment (Chl-a) concentration is not always an ideal predictor of the phytoplankton density, in our study we found that at Salpastan aggregates had significantly lower gut pigment content. We did not observe very clearly (albeit it was still the lowest) the same for solitaries, mainly because of the limited number of observations (only two), at the Salpastan location (Fig. 12). Aggregates at the APF had indistinguishable pigment contents, while solitaries at the South Georgia Basin contained roughly 3 fold less pigments in their guts compared to solitaries at 12°W survey (Fig. 12). This could be explained by any of the following factors (or combination of all): higher salp concentrations, slightly lower Chl-a levels and possibly different phytoplankton compositions in both regions. At Salpastan, *S. thompsoni* individuals were likely under the stress of very low Chl-a concentrations and potentially lower sea water temperatures, which was also reflected in their demography and biology. It seems that relationship of salps to temperature and Chl-a concentrations requires further evaluation.

On a concluding note, on the 10°E transect at 46°S the salp *Pegea confoederata* was sampled. This species has previously been known mostly from the tropics and occasionally temperate regions, generally thriving in near-coastal habitats (O'Sullivan, 1983; Esnal and Daponte, 1999). The accidental catches of this species may however extend to 37°S and 56°N within the temperature envelope of 10–28 °C according to the OBIS data set (OBIC.org.au). During our study *P. confoederata* was restricted to stations strongly influenced by the warm-core eddy (water temperatures ~9 °C) clearly observed on the temperature meridional transect along 10°E (Strass et al., in this issue) and likely represent the southernmost record of this species in the Southern Hemisphere.

Acknowledgements

We are grateful to the University of British Columbia (Canada) and the Alfred Wegener Institute for Polar and Marine Research (Germany) for providing funding allowing completion of this study. The professional and friendly support at sea by colleagues, the Capitan and the crew of the RV *Polarstern* during the ANT XXVIII/3 voyage is greatly appreciated. We would like to thank Yulia Egorova for helping to run cohort analysis. This project was partially supported by the NSERC Discovery Grant awarded to EAP. During this project B. Hunt was funded from the European Union's Seventh Framework Programme for Research, Technological Development and Demonstration under Grant agreement no. 302010 – project ISOZOO.

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