



Population dynamics of *Salpa thompsoni* near the Antarctic Peninsula: Growth rates and interannual variations in reproductive activity (1993–2009)

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ABSTRACT

The salp *Salpa thompsoni* has exhibited increased abundance in high latitude portions of the Southern Ocean in recent decades and is now frequently the numerically dominant zooplankton taxon in the Antarctic Peninsula region. The abundance increase of this species in high latitude waters is believed related to ocean warming. Due to its continuous filter feeding and production of dense rapidly sinking fecal pellets *S. thompsoni* is considered to be an important link in the export of particulate carbon from the surface waters. Hence basic information on the life history of this component of the Antarctic marine ecosystem is essential for assessing its impact given continued climate warming. Here we cover various aspects of the life history of *S. thompsoni* collected in the north Antarctic Peninsula during annual austral summer surveys of the US Antarctic Marine Living Resources (AMLR) Program between 1993 and 2009. We focus on seasonal and interannual variations in the size composition and abundance of the aggregate (sexual) and solitary (asexual) stages. This information is valuable for refining components of Southern Ocean food web models that explicitly deal with size-structured and life history information on zooplankton. Intraseasonal changes in length–frequency distribution of both stages are used to estimate their growth rates. These average 0.40 mm day^{-1} for aggregates and 0.23 mm day^{-1} for solitaries; together these represent ~ 7 week and ~ 7.5 month generation times, respectively, and a 9 month life cycle (*i.e.*, onset of aggregate production year 1 to aggregate production year 2). Based on the maximum lengths typically found during January–March, the life spans of the aggregate and solitary stages can reach at least ~ 5 and ~ 15 months, respectively. Length–frequency distributions each year reflect interannual differences in timing of the initiation and peak reproductive output. Interannual differences in the abundance of total salps and proportions of the overwintering solitary stage are significantly correlated with El Niño Southern Oscillation indices (SOI and Nino3.4) prevailing over the previous 2 years. Massive salp blooms result from two successive summers of elevated solitary production following a reversal from La Niña to El Niño conditions. These results indicate the role of basin-scale atmospheric–oceanic processes in establishing optimal conditions that support aggregate and solitary stage reproduction, development and growth.

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1. Introduction

Salps are planktonic tunicates, gelatinous organisms, present in all of the world's oceans. While seemingly primitive animals they are actually highly evolved urochordates possessing a heart, brain, eye, body muscle bands and sophisticated nervous system (Bone, 1998a,b; Godeaux et al., 1998). Under optimal conditions (*e.g.*, low chlorophyll concentrations and small food particles; Harbison et al., 1986; Ross et al., 1996; Madin et al., 2006) salps have the ability to undergo massive population blooms facilitated by an alternation of generations between sexually reproductive aggregate chain forms (blastozooids) and asexual “budding” solitary stages (oozoids; Fig. 1).

Salpa thompsoni is the most common and widespread salp in the Southern Ocean (Foxton, 1966; Casareto and Nemoto, 1986) with greatest abundance located between the Polar Front and the Southern Front of the Antarctic Circumpolar Current (ACC) (Pakhomov and McQuaid, 1996; Pakhomov and Froneman, 2004). Godeaux et al. (1998) considers this to be a clinal form (*i.e.*, exhibiting gradual phenotypic and/or genetic differences) of *Salpa fusiformis* which is broadly distributed in all waters between the subarctic and subantarctic. This clinal form is directly associated with the ACC the southern limit of which is marked by shoaling of warm Circumpolar Deep Water (CDW) and the northernmost extension of winter sea ice (Foxton, 1966; Pakhomov et al., 2011).

Salpa thompsoni has exhibited increased abundance in high latitude portions of the Southern Ocean in recent decades compared to the early 20th Century (Atkinson et al., 2004) and is now frequently the numerically dominant zooplankton taxon, at times

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represented by higher carbon biomass values than Antarctic krill (*Euphausia superba*) in the Antarctic Peninsula region (Loeb et al., 1997). The abundance increase of this filter feeding invertebrate may be due to southward movement of their distribution pattern associated with ocean warming (Pakhomov et al., 2002; Atkinson et al., 2004), compounded by latitudinal movements of the southern front of the Antarctic Circumpolar Current (Loeb et al., 2009, 2010), and thus represents a fundamental change in the marine ecosystem surrounding the Antarctic continent. Due to its swarming potential, continuous filter feeding and production of dense rapidly sinking fecal pellets *S. thompsoni* is considered to be an important link in the export of particulate carbon from surface waters to the deep sea (Fortier et al., 1994; Andersen, 1998; LeFèvre et al., 1998; Perissinotto and Pakhomov, 1998; Phillips et al., 2009). Changing abundance relationships between filter feeding salps and krill in coastal waters have significant food web implications including altered pathways that may affect apex predator populations such as marine mammals, birds and fish (LeFèvre et al., 1998; Pakhomov et al., 2002; Moline et al., 2004; Murphy et al., 2007) as well as benthic invertebrates (Gili et al., 2006). Food web alterations, in turn, impact biogeochemical cycling in Antarctic coastal waters (Walsh et al., 2001; Smetacek et al., 2004).

Because of the increasing importance of *S. thompsoni* in the coastal Antarctic marine ecosystem, basic information on its life history is essential for assessing its impact given continued climate warming. Information is available for various biological attributes including respiration, swimming, ingestion and defecation rates (Ikeda and Mitchell, 1982; Reinke, 1987; Huntley et al., 1989; Dubischar and Bathmann, 1997; Pakhomov et al., 2006; Phillips et al., 2009). Lacking, however, is information on growth rates and generation times, vital for tracking the seasonal reproductive cycles and population growth of the alternating aggregate (blastozoid) chains and solitary (oozoid) stages. Here we focus on seasonal and interannual variations in size composition and abundance of the two stages based on material in 2663 net samples collected off the eastern tip of the Antarctic Peninsula during austral summer 1993–2009 by the US Antarctic Marine Living Resources (AMLR) Program of the National Oceanographic and Atmospheric Administration (NOAA).

The goals of this study are to:

- describe seasonal and interannual variations in abundance, carbon biomass, stage composition and length–frequency characteristics of *S. thompsoni* off the north Antarctic Peninsula;

- estimate growth rates and generation times of aggregate and solitary stages using intraseasonal changes in their length–frequency distributions;
- use estimated growth rates and length–frequency distributions to define interannual differences in reproductive output (e.g., timing of the onset of chain production in spring; degree of solitary production during summer) over the 17 year time span; and
- examine interannual variations in salp abundance and maturity stage composition with respect to potential forcing by atmospheric–oceanic processes associated with ENSO.

The results of this work are used to elucidate variability of zooplankton community structure and potential food web structure near the Antarctic Peninsula. In conjunction with respiration, swimming, ingestion and defecation rate information, growth rates and generation times are directly pertinent for use in modeling efforts assessing the impacts of salp grazing activities.

1.1. General biology

Basic information on salp biology and reproduction is critical for utilizing growth rate information with respect to cycles of somatic and population growth and their ecological impacts. The two salp life stages are morphologically and anatomically distinct (Fig. 1). The tube-shaped solitary (oozoid) has a stolon that emerges during maturation and, through strobilization, forms segments (“chains”) of aggregated blastozoids. Swelling of the distal portion of the stolon indicates the developing chain that is to be released. Once the chain is released, successive blastozoid chains begin to develop proximally on the stolon. The ability to rapidly generate multiple aggregate chains gives salps the ability to produce explosive blooms under favorable conditions (Andersen, 1998). Individual aggregates (blastozoids) are more streamlined than the solitaries, with tapered ends that fit them together in the chain. The young aggregate lacks a stolon but has both an ovary and testis.

Sexual reproduction by the aggregates occurs soon after the chains are released by the solitaries. The ovary matures first so recently released aggregates are female; these are fertilized by sperm released into the water by older (now male) aggregates, with typically one egg fertilized per individual. The fertilized egg develops into an embryo attached by a placenta to the body wall (Figs. 1c and 2). Testes do not mature until the embryo has been formed thus preventing self fertilization (Godeaux et al., 1998).

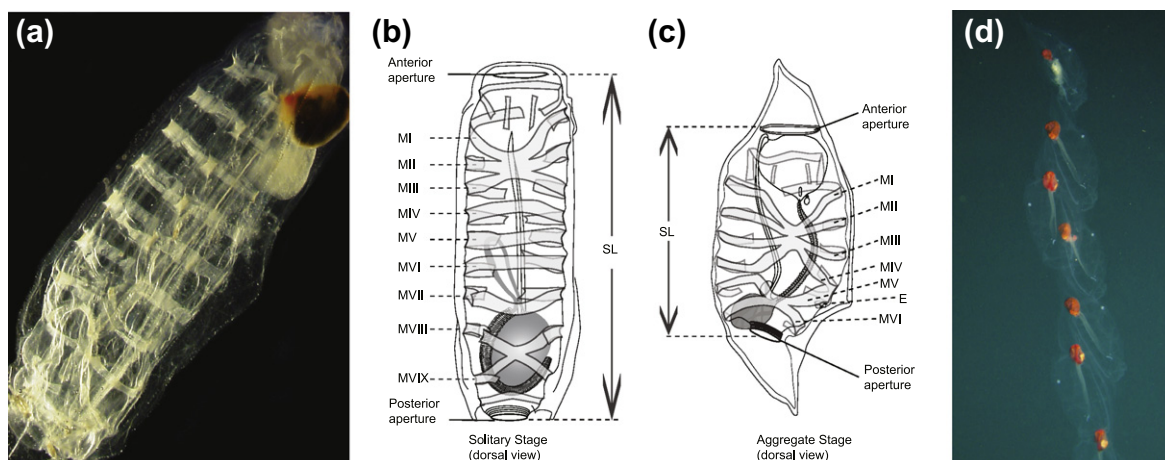


Fig. 1. Two reproductive forms of *Salpa thompsoni*: the (a) solitary (asexual, oozoid) and (b) aggregate chain (sexual, blastozoid) form. Line drawings indicate body muscle bands (M), embryonic solitary form in the blastozoid (E) and standard body length measurements. *In situ* aggregate chain photograph provided by Dirk Schories.

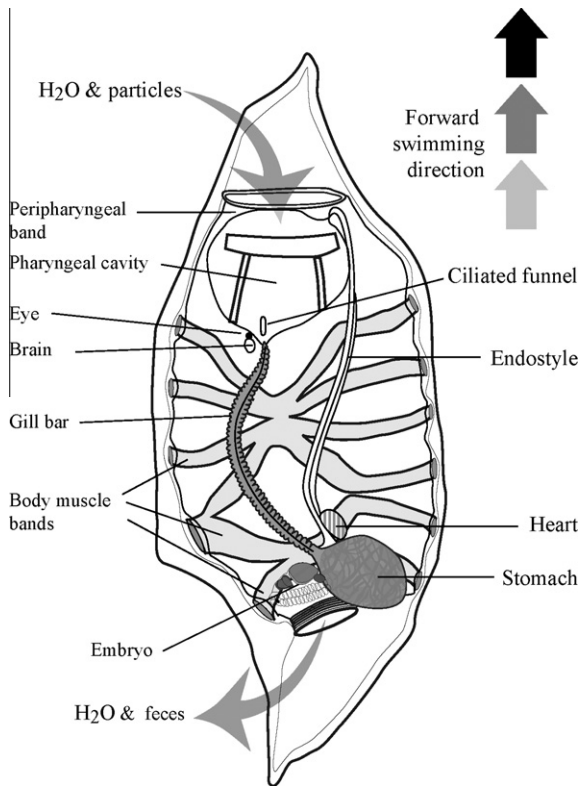


Fig. 2. Basic anatomy of *Salpa thompsoni* blastozooid (aggregate form, one individual from a chain). Continuous swimming results from regular contractions of the body muscle bands that allow water into the pharyngeal cavity through the anterior aperture and force it out as jet pulses through the posterior aperture. The endostyle produces a mucous net that fills the entire pharyngeal cavity and retains particles inhaled with the water. New mucous is continually released from the peripharyngeal band such that the baglike mucous net moves posteriorly and, along with trapped particles, is transported to the stomach where it is digested.

Salps continuously swim through jet propulsion via rhythmic contractions of the body muscle bands, alternately taking water in through their anterior (inhalant) oral aperture and forcing it out the posterior atrial aperture for forward swimming (Fig. 2); they may reverse this flow to swim backward in escape response (Bone, 1998a). As an integral part of the swimming process intake water flows through a baglike mucous net that fills the entire pharyngeal cavity. The fine mesh of this net retains particles inhaled with the water. New mucous secreted by the endostyle is continually released from the peripharyngeal band, renewing the net from the anterior end as it, along with trapped particles, is transported posteriorly to the stomach; the remains are released as dense fecal pellets that rapidly sink out of surface layers (Madin and Deibel, 1998). Salps are non-selective filter feeders, retaining particle sizes between $\sim 4 \mu\text{m}$ and $< 0.05 \mu\text{m}$ (Sutherland et al., 2010).

1.2. *Salpa thompsoni* life history overview

Foxton (1966) provided an extensive monograph on the distribution and life history of *S. thompsoni* based on material collected during the 1925–1951 Discovery Expeditions. Basic life history information for *S. thompsoni* has subsequently been augmented by Casareto and Nemoto (1986), Huntley et al. (1989), Nishikawa and Tsuda (2001) and Daponte et al. (2001). Foxton (1966) described the seasonal production cycle beginning in spring (August–September) with initiation of blastozooid chain production by large solitary forms produced the preceding summer. Peak abundance, overwhelmingly due to aggregates, occurs in the upper water column from November to March (spring to autumn)

through chain release (Fig. 3). Chain production by the solitary form is the critical factor underlying aggregate abundance as each solitary can sequentially produce up to four chains, each comprised of ~ 200 – 300 aggregates, before dying. The numbers of aggregates per chain increases with solitary size, thus over spring and summer each solitary is capable of producing a total of ~ 800 – 900 aggregates (Foxton, 1966).

Chains of small aggregate individuals occur primarily within the upper 150 m where they undergo sexual reproduction soon after release at blastozooid lengths of ~ 4 mm. The chains of aggregate individuals, along with their developing embryos (oozoids), undergo ontological descent within the water column (Fig. 3). Birth of the overwintering solitary form begins at aggregate (blastozooid) lengths of ~ 25 – 30 mm. Solitary production increases across the advancing season, with a peak in autumn (March–April). Solitary release by the aggregates occurs throughout the water column, with maximum concentrations located at 300–1000 m depths. Solitaries are released from the maternal placenta at 4–30 mm lengths and grow over winter to mature lengths of ~ 55 – 60 mm. As they grow and mature the solitaries perform an upward ontogenetic migration and initiate aggregate chain production in surface waters the following spring.

In addition to ontogenetic vertical migration, the solitary and aggregate chain forms both undergo diel vertical migrations (Foxton, 1966; Casareto and Nemoto, 1986). During summer greatest concentrations are in the upper 120 m at night and at depths > 120 m during day. According to Nishikawa and Tsuda (2001), upward migration begins mid-afternoon with elevated concentrations at 30–120 m persisting until complete darkness when largest concentrations are at 0–30 m. Downward movement to depths > 500 m begins around dawn and continues until mid-morning. These diel vertical excursions expose the individuals to a wide range of water temperatures and particulate (e.g., phytoplankton) concentrations (Pakhomov et al., 2011), both of which may modulate growth rates.

2. Methods

Data are from 1993 to 2009 austral summer surveys by the US AMLR Program (Table 1). Surveys are conducted across a fixed grid of stations spaced ~ 55 km to 110 km apart (Fig. 4). Field seasons generally included 2 month-long surveys (cruise legs) during January–February (1) and February–March (2) each year. The second cruise leg in 1997 [i.e., 1997(2)] was limited to 15 Elephant Island area samples due to mechanical problems and the 2000(1) cruise leg, primarily a multinational krill biomass survey, yielded 12 samples collected north of Livingston Island (West area) for comparison with 2000(2). Periods between survey median dates ranged from 20 days in 2000 and 45 days in 1997; the remaining surveys were separated by 27–39 days with a mean of $31 (\pm 4)$ days. Only January–February surveys were conducted during 2006, 2007 and 2009.

Zooplankton was sampled with a 1.8 m Isaacs-Kidd Midwater Trawl (IKMT) fitted with 505 m mesh plankton net and a calibrated General Oceanics flow meter. All tows were fished obliquely from 170 m or ~ 10 m above bottom in shallow waters. Tow depths were monitored with a real-time depth recorder. Tows were usually at 2 kts., ~ 20 min duration and filtered $\sim 4000 \text{ m}^3$. Fresh zooplankton samples were processed on board within two hours of net retrieval. *Euphausia superba* were enumerated for each sample and all specimens in samples with < 100 individuals were analyzed. At least 100 krill in larger samples were measured, sexed and staged according to the techniques of Makarov and Denys (1981). All salps were removed and enumerated from samples ≤ 2 L; for larger catches, abundance estimates were based on 1–2 L subsamples.

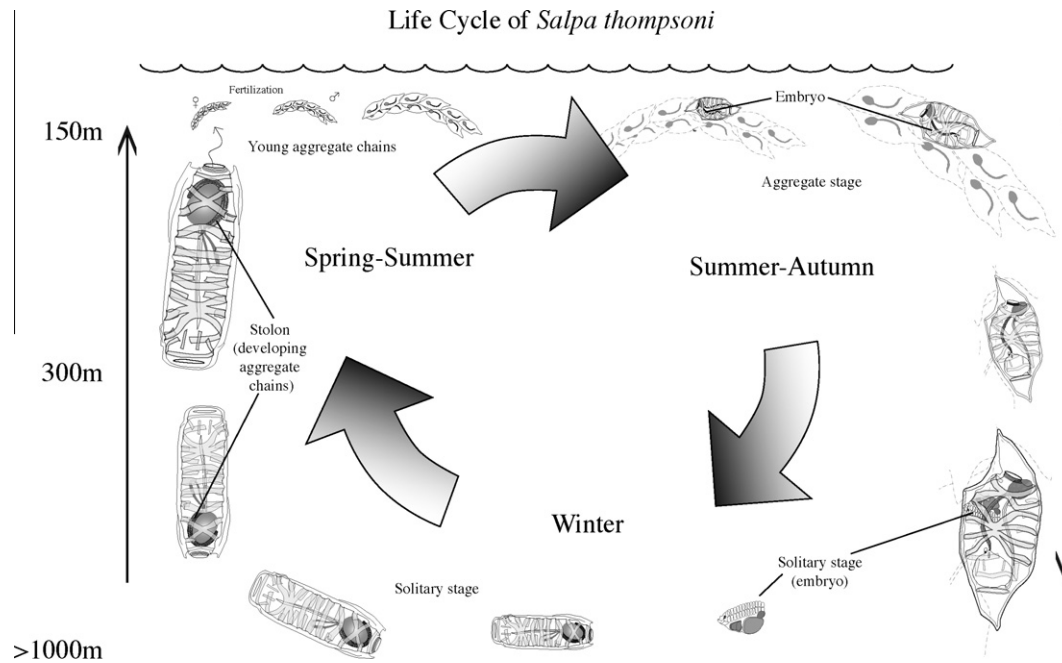


Fig. 3. Life cycle of *S. thompsoni* depicting seasonal growth, reproductive development and ontogenetic vertical migrations of the asexual solitary (oozoid) and sexual aggregate (blastozoid) chain forms based on Foxton (1966), Casareto and Nemoto (1986) and Nishikawa and Tsuda (2001).

Table 1

AMLR survey dates, 1994–2009. Leg 1 2000 survey was represented by material collected near Livingston Island (West area) and Leg 2 1997 by 15 Elephant Island area samples. No Leg 2 surveys were conducted during 2006, 2007 and 2009.

Year	Leg 1	Leg 2
1994	17 January–28 January	25 February–09 March
1995	16 January–29 January	15 February–26 February
1996	23 January–04 February	23 February–08 March
1997	26 January–09 February	16 March–24 March
1998	08 January–25 January	08 February–25 February
1999	15 January–28 January	10 February–25 February
2000	06 February–10 February	22 February–07 March
2001	15 January–30 January	12 February–02 March
2002	15 January–29 January	24 February–09 March
2003	14 January–27 January	10 February–25 February
2004	16 January–31 January	20 February–06 March
2005	17 January–30 January	22 February–09 March
2006	16 January–01 February	
2007	11 January–26 January	
2008	18 January–03 February	27 February–07 March
2009	18 January–24 January	

Total salps were enumerated in 1993 and measured in 1994 and 1995; salp maturity stage composition and aggregate and solitary stage lengths were routinely recorded from 1996 on. For samples with ≤ 100 individuals, internal body length (Foxton, 1966; Fig. 1) of all intact specimens was measured to the nearest mm; subsamples of ~ 100 individuals were measured for larger catches.

2.1. Abundance and carbon biomass

Data from the consistently and intensively sampled Elephant Island area (Fig. 4) were used to determine temporal patterns in abundance and carbon biomass. Between ~ 40 and 70 Elephant Island area stations were occupied each survey. Abundance is expressed as numbers 1000 m^{-3} water filtered with simple means, medians and standard deviations based on all samples. To be consistent with Loeb et al. (1997), carbon biomass estimates (mg C m^{-2}) for *S. thompsoni* are derived from the internal length:C

relationship presented by Huntley et al. (1989) [$C (\mu\text{g}) = 0.0013363(L)^{2.331}$] and those for krill (*Euphausia superba*) biomass utilize standard length:wet weight [weight = $0.00158 (L)^{3.40}$] and wet weight:C [$C = 72.77(W)^{1.0242}$] relationships of Kils (1981) and Nishikawa et al. (1995), respectively. Intraseasonal and interannual abundance and carbon biomass are depicted as anomalies for each of the two survey periods (i.e., deviations from the 17 year mean values for survey 1 and for survey 2).

2.2. Demographic analyses

Salp demographic analyses utilize data collected across the entire survey area in order to maximize sample size and include the full range of size and maturity stages represented during each cruise leg. Length–frequency distributions are based on numbers m^{-2} of 1 mm length categories, 4–120+ mm. In order to present salp maturity stage and size composition in relation to abundance variations, these characteristics are depicted as the mean numbers 10 m^{-2} of 1 mm categories of the aggregate and solitary forms based on samples containing salps (Figs. 5 and 6).

No direct determination of sexual maturity for the aggregate or solitary stages was made. Instead, we use length–maturity categories for both life history presented by Foxton (1966). Aggregate categories are: small, 4–14 mm, recently budded, sexually active; medium, 15–24 mm, with developing embryos; large, ≥ 25 mm, with mature embryos or spent. These are validated by results presented by Chiba et al. (1999), Daponte et al. (2001) and Pakhomov et al. (2011). Solitary categories are: small, 4–24 mm, recently born; medium, 25–54 mm, immature stolon; and large, ≥ 55 mm, mature stolon.

2.3. Aggregate stage growth rates

Because aggregates are fertilized shortly after release, the solitaries must coordinate their reproductive efforts spatially and temporally. This is facilitated through vertical diel migrations to surface layers such that newly released aggregates encounter sufficient concentrations of sperm shed by older aggregates (Purcell

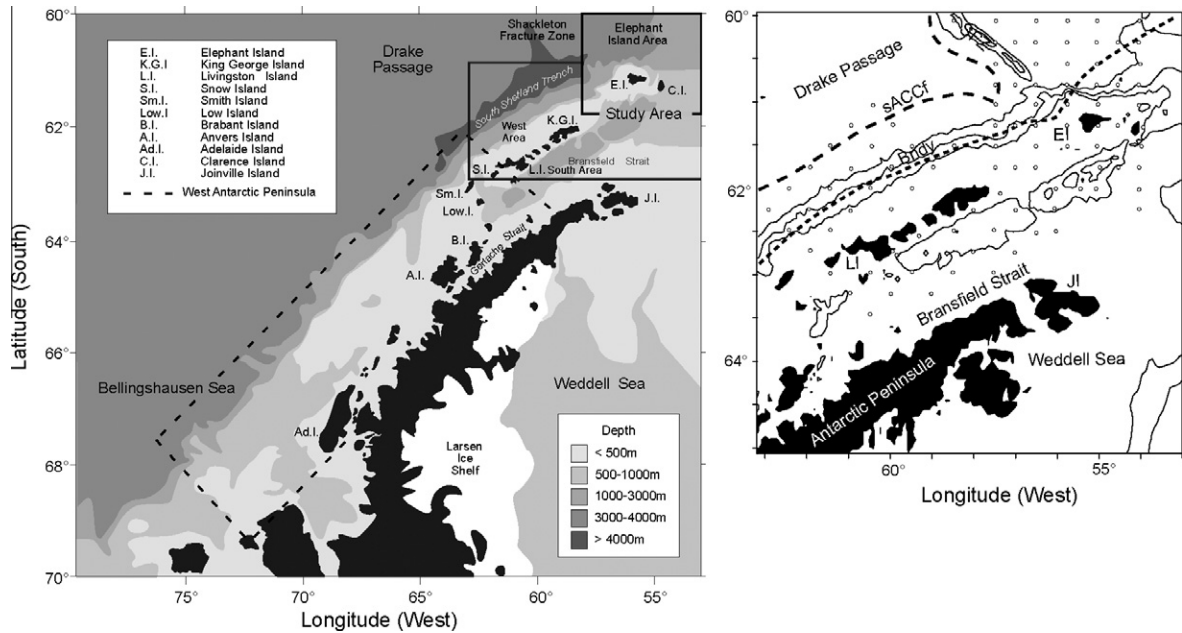


Fig. 4. (a) Location of the Antarctic Marine Living Resources (AMLR) Program survey area off the Antarctic Peninsula. (b) Standard AMLR survey grid and Elephant Island area (boxed stations) used for long-term data analyses.

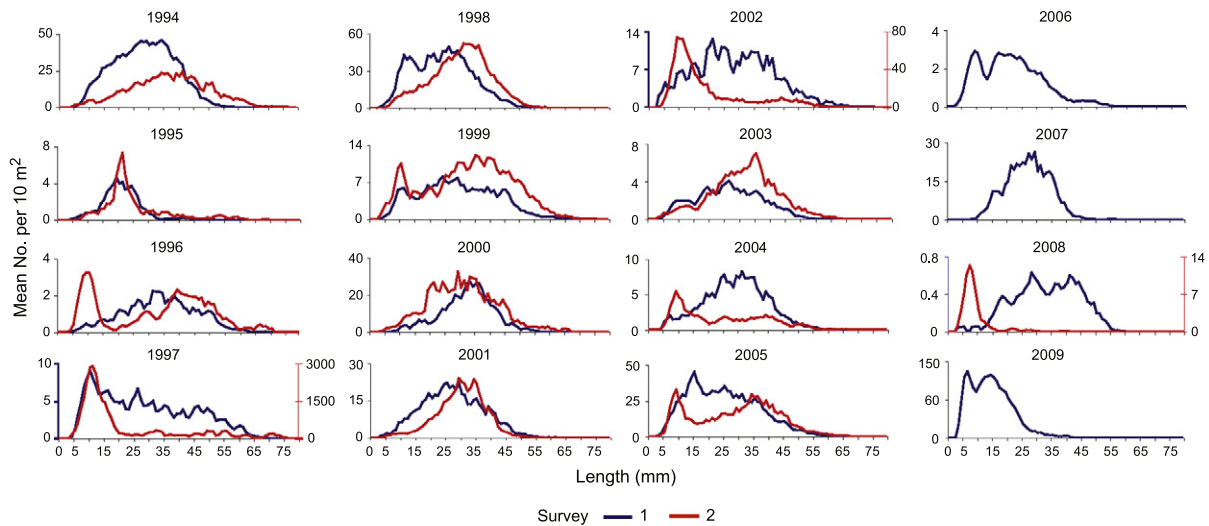


Fig. 5. Aggregate stage length distributions during (1) January–February and (2) February–March surveys, 1996–2009. The vast majority of salps <math>< 80\text{ mm}</math> in 1994 and 1995 are assumed to be aggregates. Relative abundance, based only on samples with salps, is mean numbers 10 m^{-2} represented by 1 mm length categories smoothed using a 3-point running average. Substantial intraseasonal abundance changes are indicated by a secondary Y axis.

and Madin, 1991; Miller and Cosson, 1997). Such coordination results in recognizable age cohorts and distinct length modes that can be used to assess aggregate growth rates (Heron, 1972; Heron and Benham, 1984; Tsuda and Nemoto, 1992; Miller and Cosson, 1997). All length/maturity stages of *S. thompsoni* aggregates are represented in the upper water column (Foxton, 1966; Casareto and Nemoto, 1986) and, due to their relatively long generation time, it is possible to track one or more of the cohort length modes over the summer season.

Aggregate growth rates were derived from changes in distinct size modes represented across the study area during back-to-back surveys each year. Because the aggregate stage typically was represented by polymodal length–frequency distributions each survey (Fig. 5) cluster analysis was used to identify size modes of various

cohorts contributing to these overall patterns. Cluster analysis was applied to length–frequency data (1 mm increments) from samples represented by >40 individuals each cruise leg. Cluster analysis utilized Euclidean distance and Ward’s linkage method with length–frequency clusters distinguished by a distance of ≥ 0.60 (Legendre and Legendre, 1998). Growth rates were derived from length–frequency distributions of individual clusters (e.g., January 2005 Cluster 1, February 2005 Cluster 1; Fig. 7a and b) smoothed by a three point running average. As indicated in Fig. 7a and b, the length–frequency distributions of individual clusters identified during the first survey were advanced to approximate those of clusters identified during the second survey, with subsequent evaluation of changes in distinct length modes (mm) over the time (days) between median survey dates.

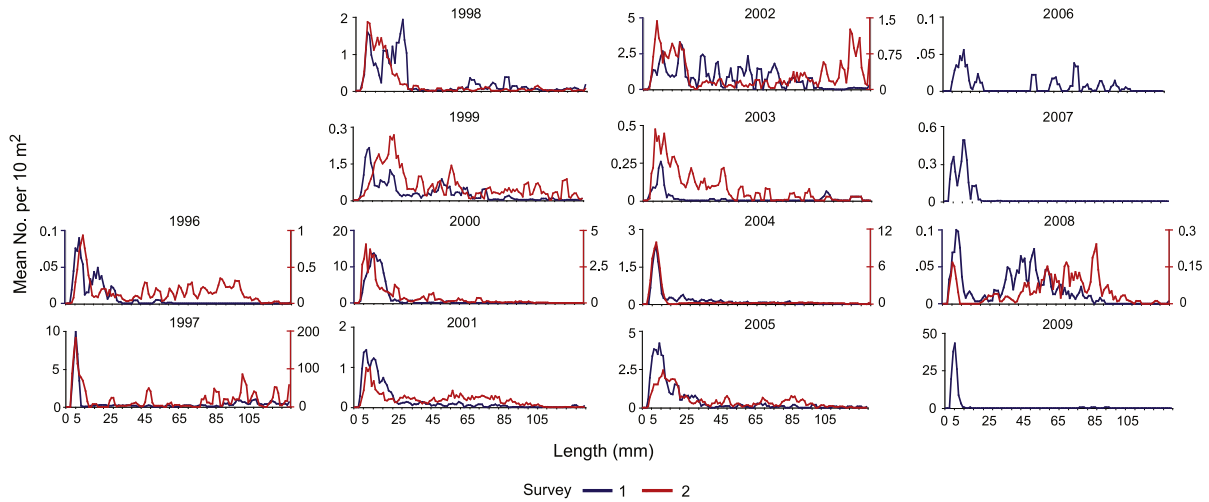


Fig. 6. Solitary stage length distributions during (1) January–February and (2) February–March surveys, 1996–2009. Relative abundance, based only on samples with salps, is mean numbers 10 m^{-2} represented by 1 mm length categories after smoothing using a 3-point running average. Substantial intraseasonal abundance changes are indicated by a secondary Y axis.

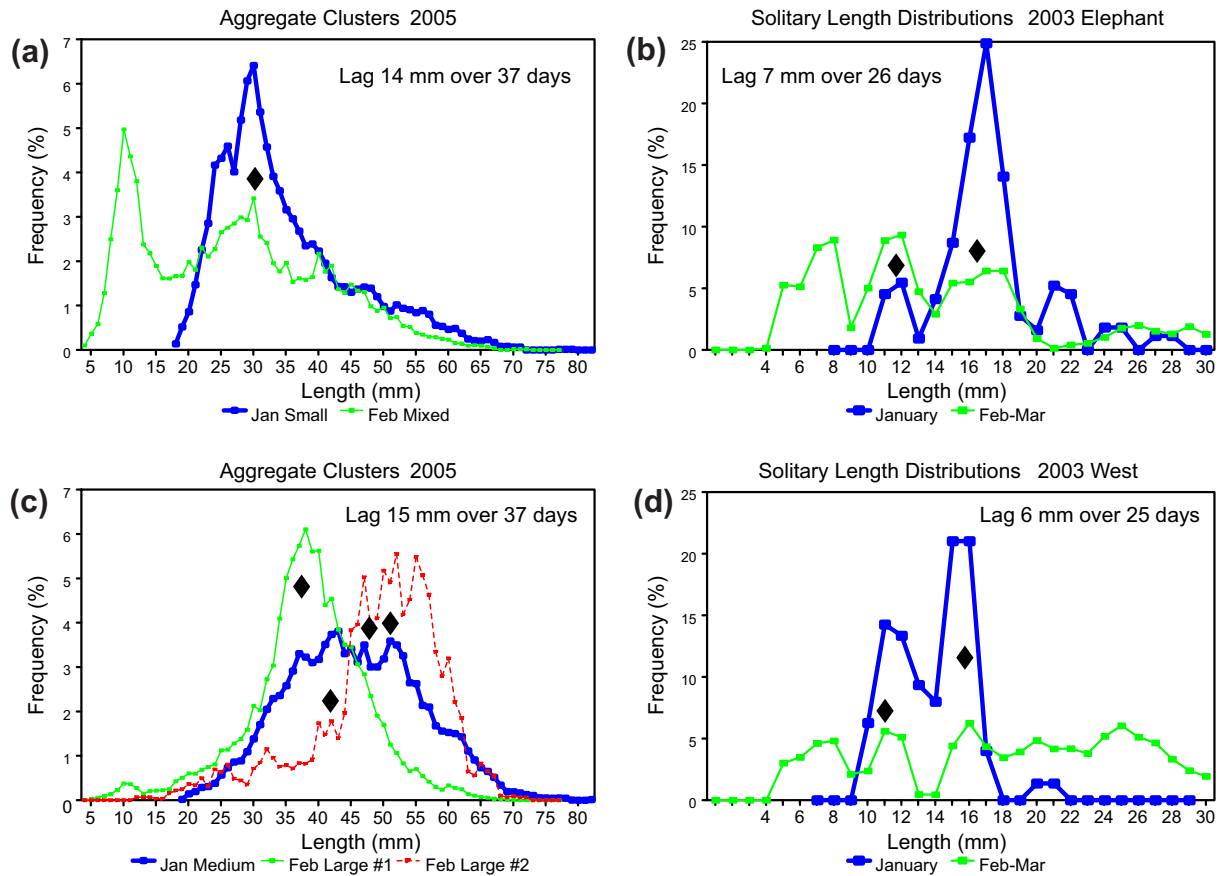


Fig. 7. Examples of (a and b) aggregate and (c and d) solitary stage length–frequency distributions and size modes used for growth rate estimates. For the aggregate stage, cluster analysis identified distinct length modes included in polymodal length–frequency distributions represented each survey (Fig. 5). The length–frequency distributions of individual clusters identified during leg 1 (e.g., January Cluster 1, Cluster 2) were advanced to approximate those of clusters identified during leg 2 (e.g., February Cluster 1, Cluster 2, Cluster 3). For the solitary stage, length modes of individuals $<30\text{ mm}$ (Fig. 6) were used because of their relatively constant presence in the upper water column; comparisons were made between specimens collected within separate sampling areas due to their limited spatial distributions. For both stages, corresponding length modes from back to back surveys (indicated by diamonds) were used to estimate the amount of change in mm over the median number of days between each survey effort.

2.4. Solitary stage growth rates

During summer the solitary stage is vastly outnumbered by aggregates and its presence in surface layers is impacted by

ontogenetic and diel vertical migrations (Foxton, 1966) as well as water column structure and influence of CDW (Pakhomov et al., 2011). Our data indicate that small solitaries (e.g., $<30\text{ mm}$) are present in the upper water column during day and night, reflecting

relatively limited diel vertical migrations, and that these demonstrate increased size across the summer surveys (Fig. 6). Our data also indicate a more limited spatial distribution of this stage compared to the aggregates. As a consequence, solitary stage growth rates were estimated from the change in length–frequency distributions and length modes of recently born individuals (*i.e.*, ≤ 30 mm) within a geographic locale (*e.g.*, Elephant Island, West and South areas; Fig. 4). Exceptions to single area comparisons were 1997 when relatively abundant solitaries in the South and West areas during January were examined with respect to those present in the Elephant Island area in March. As for the aggregate stage, comparisons were based on data smoothed by a three point running average with the time interval derived from the median date of back-to-back cruise legs within each area (Fig. 7c and d).

2.5. Environmental correlations with salp growth and abundance

Interannual and longer term abundance variations of *S. thompsoni* and *E. superba* have been linked to basin-scale El Niño–Southern Oscillation (ENSO) forcing via the Pacific South American pattern of sea level pressure (PSA) and the Antarctic Dipole pattern of sea surface temperature (Yuan, 2004; Loeb et al., 2009, 2010). Using the 1980–2004 Elephant Island area data set Loeb et al. (2009, 2010) established significant correlations between biological variables in the Antarctic Peninsula region and the SOI at 0- and 1-year lags. Although mean abundance of *S. thompsoni* was not directly correlated with SOI in those studies, it had a significant negative correlation with winter sea ice which, in turn, is negatively correlated with SOI.

Here we further examine the potential role of longer-term ENSO forcing on the abundance and, for the first time, demography of *S. thompsoni*. This is done through Kendall's Tau (*T*) correlation analysis between mean salp abundance values (total salps, aggregate and solitary stages) and percent contribution by solitaries during each cruise leg and 3-month running average values of the Southern Oscillation Index (SOI) and Nino 3.4 Index. Correlations were done with summer (January–March; *i.e.*, the field season), fall (April–June), winter (July–September) and spring (October–December) SOI and Nino3.4 Index values lagged by 1 and 2 years (*i.e.*, 3, 6, 9, 12, 15, 18, 21 and 24 month lags) to assess the long-term implications of ENSO forcing. SOI and Nino3.4 data were obtained from the NOAA climate prediction center (www.cpc.noaa.gov/data/indices/NCEP/NCAR; Kalnay et al., 1996).

3. Results

3.1. Abundance

Mean summertime abundance of total *S. thompsoni* in the Elephant Island area varied by generally two orders of magnitude between lows in 1995, 1996, 2003, 2006 and 2008 ($18.2\text{--}40.6 \times 1000 \text{ m}^{-3}$) and highs in 1993, 1998, 2005 and 2009 ($702.0\text{--}1395.5 \times 1000 \text{ m}^{-3}$). Median concentrations ranged almost three orders of magnitude from 1995, 1996, 2003, 2006–2008 lows ($0.8\text{--}8.2 \times 1000 \text{ m}^{-3}$) to 1993, 1994, 1998, 2005 and 2009 highs ($326.4\text{--}453.8 \times 1000 \text{ m}^{-3}$). Overall concentrations in 1993, 1998 and 2009 were significantly larger than all other years except 2005, and those of 2005 were significantly larger than during 1995, 1996, 2003 and 2008 (ANOVA, $P < 0.05$). There was no apparent trend for increased or decreased abundance over the 1993–2009 period (Fig. 8a). This is supported by a nonsignificant regression of salp abundance vs. year ($N = 34$, $R = 0.22$, $F = 1.69$, $P = 0.20$).

Salp abundance in the Elephant Island area did not show consistent changes with advancing season. Increased abundance from early to late summer occurred during seven of 13 years and decreased abundance was observed during 4 years; 2 years had little change (Table 2). When present, intraseasonal changes in mean concentrations were generally modest ($< 2\times$). Major exceptions were a significant 50% abundance decrease during 1994 and significantly increased abundance ($> 5\times$) during 1997 and 2008 (ANOVA, $P < 0.05$). In contrast, median abundance decreased by 20–60% during 8 years; exceptions were 1993, 1997, 1998, and 2002 when medians had 1.6–6.1 \times increases and 1999 when there was little change. Overall mean ($\pm 1\text{SD}$) and median survey values were 446.1 (± 1239.7) and 98.1 individuals 1000 m^{-3} , respectively. Over the 17 year data set, there were four periods with anomalously high salp concentrations: 1993–1994, 1997–1998, 2005 and 2009 (Fig. 8a).

Intraseasonal and interannual changes in salp carbon biomass values in the Elephant Island area (Table 3; Fig. 8b) reflected mean and median abundance variations ($N = 28$, $T = 0.78$, $P < 0.001$). Lowest mean biomass during 1995 and 2008 surveys ranged from 5.8 to 13.1 mg C m^{-2} compared to highs of 334.5–1139.7 mg C m^{-2} during 1994, 1997, 1998 and 2005. Size composition was a compounding factor influencing biomass during some years. Predominantly small salps sampled during 2009(1) yielded relatively low carbon biomass despite extremely high concentrations while

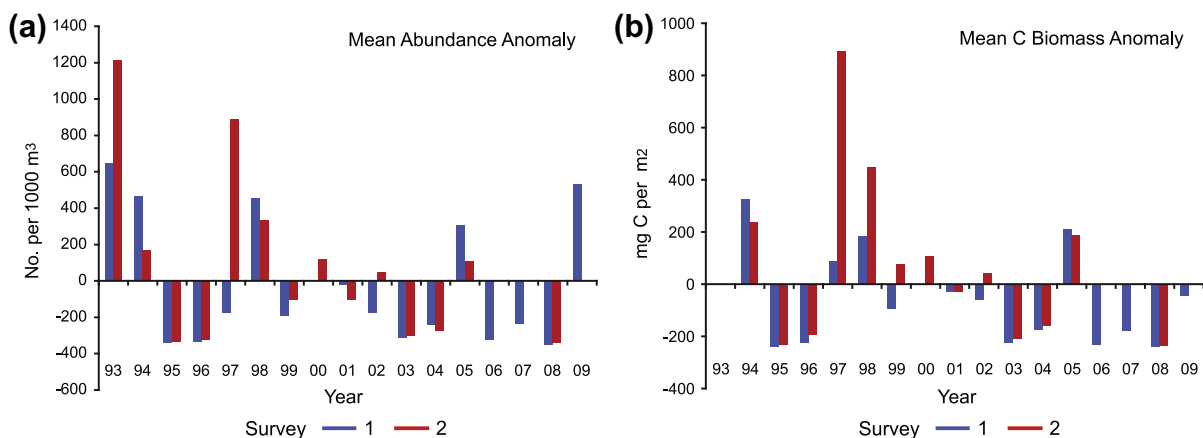


Fig. 8. Intra-seasonal and inter-annual abundance fluctuations of *Salpa thompsoni* (aggregate and solitary stages combined) in the Elephant Island area, 1993–2009, showing anomalies of mean (a) abundance and (b) carbon biomass values during each cruise leg. Lack of salp size information from 1993 precludes carbon biomass estimates for those surveys.

Table 2
Abundance statistics for *Salpa thompsoni* collected in the Elephant Island area during summer surveys, 1993–2009. *N* is number of samples. Abundance expressed as mean, standard deviation, median and maximum numbers 1000 m⁻³ filtered. Data from 12 stations north of Livingston Island (West area) used for 2000(1).

	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009
Survey	January–February																
N	70	63	71	72	71	61	40	12.	60	44	38	46	48	48	48	34	47
Mean	1213.3	931.9	20.2	25.5	222.1	939.7	197.5	266.6	401.3	263.7	39.8	113.3	777.5	40.6	115.4	5.2	1334.5
SD	2536.9	957.9	46.8	36.6	339.4	1569.2	194.0	397.9	373.4	399.9	86.5	108.4	828.6	64.8	264.7	7.3	297.4
Med	245.8	582.3	1.6	10.1	85.6	348.9	159.1	64.3	289.0	55.2	5.6	86.3	431.5	6.0	2.5	2.6	453.8
Max	16078.8	4781.7	239.9	161.6	2006.3	8030.4	873.4	1417.8	2259.3	1811.9	456.2	485.5	3230.7	322.4	1113.5	29.7	18485.7
Survey	February–March																
N	67	70	71	72	16	61	39	60	57	44	48	47	48	n.a.	n.a.	44	n.a.
Mean	1585.9	495.1	20.6	33.2	1243.8	977.3	309.2	587.2	290.3	366.9	39.1	86.7	553.8	–	–	28.2	–
SD	2746.0	583.5	66.9	86.3	1266.0	1508.9	380.9	2202.3	325.4	509.0	77.8	127.6	721.4	–	–	60.0	–
Med	469.0	242.6	0.7	5.6	521.0	553.8	162.5	169.1	200.7	186.5	4.5	35.0	317.2	–	–	1.3	–
Max	16662.5	2377.5	391.9	659.4	4348.3	10712.9	1550.2	15458.4	1554.6	1867.8	305.8	662.9	3473.5	–	–	238.8	–

Table 3
Carbon biomass values (mg Cm⁻²) of *Salpa thompsoni* in the Elephant Island area during summer surveys, 1994–2009. Data from 12 stations north of Livingston Island (West area) used for 2000(1). Salp:Krill is ratio of the median carbon biomass represented by salps and *Euphausia superba* (Antarctic krill) in the Elephant Island area.

Year	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009
	January–February															
N	63	57	72	71	61	40	12	60	44	38	46	48	48	48	34	47
Mean	570.6	7.8	20.2	334.5	430.8	151.8	128.8	215.2	184.8	22.8	72.1	455.2	15.5	69.2	5.8	199.4
SD	563.2	16.1	30.9	1115.6	565.3	166.1	183.9	175.5	269.1	45.0	81.3	495.2	24.8	161.0	11.4	322.9
Med	400.5	1.3	10.0	108.9	187.0	93.2	23.1	161.9	81.7	2.7	54.6	264.8	2.3	0.9	2.3	72.7
Max	3276.8	75.3	134.2	9434.6	2699.0	882.7	583.7	897.4	1193.5	249.9	404.0	2007.6	123.2	816.9	61.2	1691.9
Salp:Krill	15.6	0.03	0.14	2.4	4.0	6.4	n.a.	2.8	3.4	0.03	3.0	2.4	0.02	0.005	0.02	2.9
	February–March															
N	70	71	72	16	61	39	60	57	44	48	47	48	–	–	44	–
Mean	483.5	13.1	50.7	1139.7	694.6	321.9	352.3	214.8	286.7	39.1	86.3	433.3	–	–	10.1	–
SD	469.4	47.3	146.5	1269.8	1121.2	335.1	1368.5	226.7	316.2	82.3	157.1	532.3	–	–	17.7	–
Med	284.0	0.7	4.6	504.8	379.4	193.5	115.5	139.1	233.9	2.0	27.3	301.3	–	–	2.7	–
Max	1843.6	325.2	954.0	4645.4	8543.0	1698.1	10549.3	1095.3	1091.6	354.0	863.1	3511.2	–	–	78.4	–
Salp:Krill	102.0	0.05	0.11	10.1	12.0	28.0	3.8	4.1	137.6	0.11	0.52	19.6	n.a.	n.a.	0.03	n.a.

elevated biomass in 1997 reflected substantial numbers of large solitary forms (Table 4). Size was also a factor in 1995, 1998, 2001 and 2003 when aggregate length (Table 4) and mean biomass increased while mean abundance remained stable or decreased between the two surveys. Median salp carbon biomass values surpassed those of krill during 17 of 28 surveys (61%); exceptions occurred primarily during the 1995–1996, 2003 and 2006–2008 periods of relatively low salp abundance.

3.2. Stage and size composition

Aggregates numerically dominated the catches and generally comprised >93% of individuals collected during each survey (legs 1 and 2; Table 4). Exceptions occurred during 8 of the 28 cruise legs when solitaries made up between 7.1% and 43.6% of total salps. Large proportions of solitaries in 1996(2) preceded anomalously high mean solitary abundance in 1997(1,2) and high mean aggregate abundance in 1997(2) and 1998(1,2). Similarly, large proportions of solitaries in 2004(2) and 2008(1,2) preceded anomalously large concentrations of both stages in 2005 and 2009 (Fig. 9). In contrast, moderately elevated proportions of solitaries in 2000(2) and 2003(2) were followed by low salp abundance the following years. These observations are supported by a significant correlation between proportions of solitary salps during February–March surveys and numbers of solitaries the following February–March ($N = 9$, $T = +0.67$, $P = 0.01$).

Aggregate length–frequency distributions varied widely from year to year (Fig. 5). During most years 99% of individuals had internal body lengths ≤ 62 mm. Almost all surveys were characterized by

polymodal length distributions indicative of pulsed production across spring and summer months.

The maximum aggregate length and continuous (*i.e.*, uninterrupted) size range were strongly correlated ($N = 25$, $T = 0.64$, $P \ll 0.001$) supporting their use as indicators of the duration of seasonal chain production. This is a very valuable tool for evaluating reproductive output. Largest individuals (72–90 mm) and broadest continuous size ranges (>60 mm) were exhibited during 1996, 1997, 1999, 2000, 2002 and 2005. Extremely large aggregates (82–90 mm) were collected only in 1997 and 1999. Elevated numbers of newly released aggregates during February–March 1996, 1997, 1999, 2002, 2004, 2005 and 2008 (Fig. 5) indicated late season chain production. Late season chain production was particularly extreme in 1997 and 2008 when mean numbers of individuals <15 mm in length increased by 240 \times and 120 \times , respectively. The most limited size ranges occurred during 1995 when length–frequency distributions suggest two relatively brief periods of production (Fig. 5). Relatively short aggregate production periods also occurred during 1994, 1998, 2001 and 2003.

Solitaries were typically represented by a broad size range with maximum lengths >100 mm found during most surveys (Table 4, Fig. 6). Extremely large solitaries (>160 mm) were collected only during 1996 and 1997. Typically, 99% of solitaries sampled each year were ≤ 115 mm. Recently released solitaries were relatively abundant during all January–February surveys indicating their production during late spring and early summer. Concentrations of all three length/maturity categories increased with advancing season during seven of 11 years with back-to-back surveys while concentrations of medium and large stages increased during three additional surveys. Intraseasonal reduction in numbers of medium

Table 4

Demographic statistics for the two maturity stages of *Salpa thompsoni* sampled, 1994–2009. Both stages are pooled for 1994 and 1995 (ALL) and treated as aggregates. *N* is number of samples represented by salps each cruise. % Total is the proportion of total salps represented by aggregate and solitary stages; stages were not identified in 1994 or 1995. For aggregates the continuous (uninterrupted) length range (mm) and maximum lengths suggest their early seasonal production history. For both stages median and modal lengths (mm) and relative proportions of small (recently released), medium (developing embryo/stolon) and large (mature embryo/stolon) stages reflect production within each survey period. Italic values exhibited massive salp blooms. The 2000(1) data are derived from a limited sampling effort north of Livingston Island (West area).

Year	Stage	January–February								February–March											
		N	% Total	Length (mm)				Stage composition (%)			N	% Total	Length (mm)				Stage composition (%)				
				Continuous range	Max	Med	Mode	Small range	Medium	Large			Continuous range	Max	Med	Mode	Small	Medium	Large		
1994	ALL	81	n.a	6–57		28	28	9.7	26.5	63.8	89	n.a	4–76		37	40	4.6	13.1	82.3		
1995	ALL	41	n.a	4–47		20	20	12.2	63.1	24.7	40	n.a	7–48		22	20	7.8	58.5	33.7		
1996	AGG	55	98.5	5–62		72	33	32	6.2	16.1	77.7	49	78.9	5–69		69	37	10	28.9	4.1	67.0
	SOL		1.5			>120	12	8	89.0	10.1	0.9		21.1		>120	48	9	36.9	17.1	46.0	
1997	AGG	105	80.3	4–69		84	26	9	24.8	20.5	54.7	16	92.9	4–66		82	13	11	58.6	15.7	25.7
	SOL		19.7			>120	10	5	54.3	6.8	38.9		7.1		>120	65	4	37.0	10.6	52.4	
1998	AGG	104	97.5	4–56		59	24	25	21.6	30.5	47.8	104	98.0	6–60		60	31	32	7.2	19.7	73.1
	SOL		2.5			>120	20	25	67.2	12.4	20.4		2.0		>120	12	7	85.3	6.8	7.9	
1999	AGG	75	94.5	4–65		70	28	28	15.7	23.7	60.6	67	93.4	4–72		90	34	40	15.3	13.1	71.6
	SOL		5.5			>120	20	9	55.1	28.1	16.8		6.6		>120	32	20	42.3	27.2	30.6	
2000	AGG	12	77.3	8–55		55	33	32	3.2	14.1	82.7	95	94.2	4–73		78	30	30	6.8	24.1	69.1
	SOL		22.7			>120	63	11	96.6	3.1	0.3		5.8		116	11	5	73.7	16.3	10.0	
2001	AGG	101	96.5	4–62		66	26	28	11.2	30.5	58.3	96	94.9	4–56		63	30	30	4.1	18.6	77.3
	SOL		3.5			>120	11	5	79.4	12.5	8.1		5.1		117	39	7	38.3	28.0	33.7	
2002	AGG	79	97.5	4–68		75	28	20	15.6	25.2	59.2	69	95.9	4–63		74	13	10	54.5	22.0	23.5
	SOL		2.5			>120	38	20	34.6	33.9	31.6		4.1		>120	58	110	40.6	8.4	51.0	
2003	AGG	56	98.2	4–53		55	26	25	16.2	27.3	56.5	60	93.7	4–63		63	32	36	7.8	17.3	74.9
	SOL		1.8			113	10	9	75.0	3.2	21.8		6.3		113	19	7	56.6	30.5	12.9	
2004	AGG	84	91.5	4–61		67	29	30	8.9	23.9	67.2	85	56.4	4–56		67	22	10	37.3	16.8	45.8
	SOL		8.5			>120	9	6	72.5	17.9	9.6		43.6		>120	8	6	78.6	8.1	13.3	
2005	AGG	97	95.5	4–65		68	24	14	22.1	30.6	47.4	89	93.9	4–68		70	31	35	22.6	13.8	63.6
	SOL		4.5			>120	11	10	80.5	11.9	7.6		6.1		114	19	10	57.4	17.0	25.5	
2006	AGG	56	98.9	4–55		55	20	10	28.1	37.1	34.8										
	SOL		1.1			100	20	72	51.1	8.4	40.5										
2007	AGG	43	99.2	5–51		55	27	28	4.2	34.1	61.7										
	SOL		0.8			29	10	11	99.5	0.5	0.0										
2008	AGG	42	88.3	4–56		58	33	29	3.3	20.0	76.7	29	91.9	4–42		68	7	8	93.9	3.5	2.6
	SOL		11.7			>120	40	8	30.0	48.8	21.2		8.1		113	64	80	12.1	22.9	65.0	
2009	AGG	80	92.6	4–57		75	14	6	55.5	36.8	7.7										
	SOL		7.4			115	5	4	98.0	0.1	1.9										

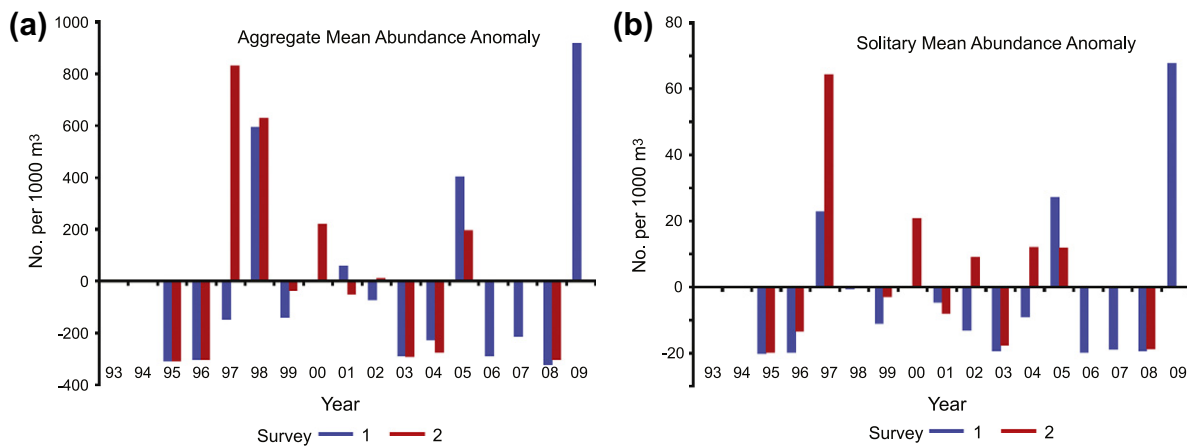


Fig. 9. Mean abundance anomalies of (a) aggregate and (b) solitary stage *Salpa thompsoni* in the total survey area, 1995–2009.

and large solitaries occurred only during 1998; reduction of small individuals occurred in 2000, 2001 and 2005. Recently born and mature sized solitaries were fairly equally represented during 1996(2), 1997(1,2) and 2008(1). In 2004(1,2) and 2009(1) the majority of solitaries were recently born representing elevated, seasonally advanced production by the aggregates stage; in 2008(2) the majority of solitaries were large mature forms exerting a late season pulse of aggregate production. As noted above 1996(2), 1997(1,2), 2004(1,2), 2008(1,2) and 2009(1) were

characterized by unusually large contributions of solitaries to the total salp catch. All of these cases occurred either the year before or during periods of massive salp blooms.

When population structures of the aggregate and solitary stages are examined together (Table 4; Figs. 5 and 6) both demonstrated increased reproduction with advancing season (i.e., prolonged production periods) during 1996, 1997, 1999, 2002, 2004 and 2008. Despite seasonal increases in concentrations of both large aggregate and solitary forms, increased production was limited to small

Table 5

Salpa thompsoni growth rates estimated from length mode changes between back-to-back surveys, 1995–2005. Rates are mm day⁻¹ based on changes over the median number of days separating each survey effort. *N* is number of between-survey length mode comparisons each year. Blanks indicate years when changes in distinct length modes could not be determined. Asterisks (**) denote significantly higher solitary growth rates after 2000 (ANOVA, $P < 0.01$).

Year	Aggregate stage				Solitary stage			
	<i>N</i>	Range	Mean	SD	<i>N</i>	Range	Mean	SD
1995	10	0.31–0.45	0.38	0.04				
1996	12	0.32–0.45	0.39	0.05				
1997					4	0.18–0.22	0.20	0.02
1998	8	0.35–0.48	0.44	0.05	6	0.16–0.26	0.21	0.04
1999	20	0.33–0.52	0.43	0.06	7	0.15–0.23	0.17	0.03
2000	9	0.25–0.50	0.38	0.09	3	0.19–0.25	0.23	0.03
2001					6	0.26–0.29	0.28	0.01
2002	11	0.33–0.44	0.38	0.04	3	0.23–0.26	0.25	0.02
2003	8	0.38–0.46	0.39	0.02	6	0.23–0.28	0.26	0.02
2005	9	0.35–0.43	0.39	0.03	3	0.21–0.23	0.22	0.01
1995–2005	87	0.25–0.52	0.40	0.05	38	0.15–0.29	0.23	0.04
1995–2000	59	0.25–0.52	0.41	0.06	20	0.15–0.26	0.20	0.04
2001–2005	28	0.33–0.43	0.39	0.03	18	**0.21–0.29	0.26	0.03

aggregates in 2000 and small solitaries in 2003. Minimal late season production of both aggregates and solitaries occurred during 1998, 2001 and 2005 suggesting unfavorable conditions during those times. Of note are substantial intraseasonal abundance increases of all sizes of solitaries in 1996, of aggregates and solitaries in 1997, and of medium sized solitaries in 2003. These results suggest the importance of advective transport of individuals into and out of the survey area and vertical migration between the upper water column and greater depths, as well as reproduction, underlying intraseasonal abundance fluctuations of both forms.

3.3. Growth rates

Aggregate stage growth rate estimates were made possible by tracking changes in length–frequency distribution patterns and length modes across the survey area during eight field seasons (Table 5). Aggregate growth rates within each field season examined ranged from 0.25 to 0.52 mm day⁻¹ with overall means of 0.38–0.44 mm day⁻¹. The greatest variability (0.38 ± 0.09 SD) mm day⁻¹ occurred during 2000 when lengths obtained from limited sampling in the West area leg 1 were compared to those represented in the broader survey area sampled leg 2. The overall mean growth rate derived from 87 length mode comparisons was 0.40 (± 0.05) mm day⁻¹ or ~ 12 mm month⁻¹.

Solitary growth rate estimates were obtained from length increases of individuals ≤ 30 mm within geographic areas sampled during eight field seasons. Growth rate estimates ranged from 0.15 to 0.29 mm day⁻¹, with overall means of 0.17–0.28 mm day⁻¹. The 38 length mode comparisons yielded a mean of 0.23 (± 0.04 SD) mm day⁻¹, ~ 7 mm month⁻¹. Interestingly, the estimated growth rate from 1997 to 2000 ($N = 20$, mean 0.20 ± 0.04 mm day⁻¹) was significantly lower than that from 2001 to 2005 ($N = 18$, mean 0.26 ± 0.03 mm day⁻¹; ANOVA $P < 0.01$). No such difference occurred for the aggregate stage.

3.4. Generation times and life spans

Based on a $0.40 (\pm 0.05)$ mm day⁻¹ growth rate the recently released, and potentially sexually active, aggregate stage lasts on average 27 days (Fig. 10a; Table 6). Embryonic development resulting from successful fertilization would take another 25 days. The period from aggregate production to solitary birth would therefore average 52 days, slightly less than 2 months (Fig. 10a). On average, aggregates attaining lengths of 62 mm, typically the largest sizes represented during January–March surveys, were released by solitaries ~ 146 days earlier (August–October). These individuals indicate aggregate life spans approaching 5 months. The extremely large aggregates found in 1997 and 1999 (82–90 mm) would likely have been produced during mid-July to early August suggesting a very early onset of reproduction and maximum life span of ~ 7 months.

With a growth rate of $0.23 (\pm 0.04)$ mm day⁻¹ the solitary stage would require, on average, 91 days to reach lengths associated with stolon development and another 131 days to attain reproductively mature lengths of 55 mm, resulting in a total of 222 generational days (~ 7.5 months) between birth and the onset of chain release. Under this scenario, solitaries released during January and February are capable of chain production the following August and September, while the largest solitaries (*i.e.*, 115 mm) typically observed in January–February would have resulted from release in October–November, 15 months earlier. The huge solitary forms collected in 1996 and 1997 (to 180 mm) likely represent individuals that were born in December–February 2 years before, suggesting a maximum life span of at least 2 years.

3.5. Interannual variability in reproduction

Based on the largest aggregate individuals recorded each field season, the seasonal onset of chain release ranged from mid-July to mid-September (Fig. 11). Earliest release occurred from

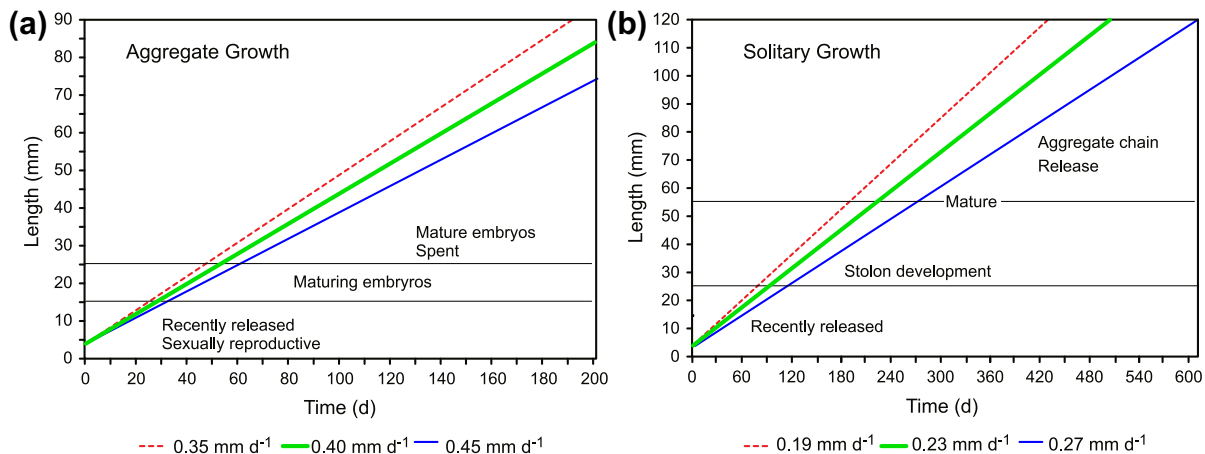


Fig. 10. Developmental time lines for (a) aggregate and (b) solitary stages of *Salpa thompsoni* based on their respective growth rate estimates (means ± 1 standard deviation).

Table 6

Developmental schedules (days) for aggregate and solitary stages of *Salpa thompsoni* derived from their respective growth rate estimates (mean \pm 1 SD). Generation times for each are from time of release to reproductive production based on internal body length. Life cycle duration is from the initiation of aggregate release by solitaries in spring to the initiation of solitary release by aggregates in fall. Age estimates are provided for maximum lengths typically represented by 99% of individuals each survey and for the largest individuals collected during AMLR surveys.

Developmental stage	Aggregate stage (days)		Developmental stage (days)	Solitary stage		Life cycle (days)	
	Mean	Range		Mean	Range	Mean	Range
Recently released/ Sexually reproductive	27	(24–31)					
Maturing embryos	25	(23–28)					
Mature	52	(47–59)	Recently released	91	(77–110)		
Growth to 62 mm	146	(130–166)	Stolon development	131	(111–158)		
Maximum @ 90 mm	215	(191–246)	Mature	222	(188–268)	274	(235–327)
			Growth to 115 mm	483	(411–584)		
			Maximum @ 180 m	766	(652–926)		

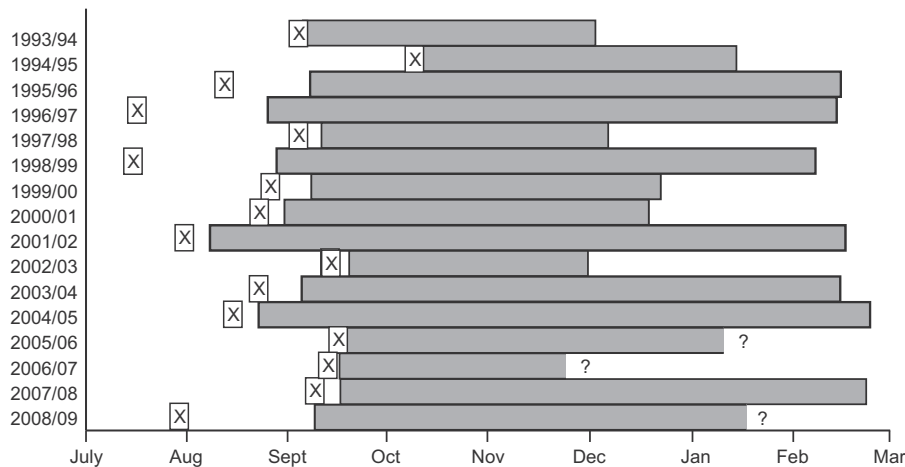


Fig. 11. Approximate timing of aggregate chain production, 1993–2009, based on mean growth rate estimates and survey demographics presented in Table 4. Initiation of chain production (X) and continuous (uninterrupted) chain production (filled bars) are based, respectively, on the largest aggregate size observed each year and continuous size range observed each survey. Duration of peak chain production is based on modal lengths observed during leg 2 each year and therefore does not apply to 2006, 2007 and 2009 which had only one January–February survey.

mid- to late July 1996, 1998, 2001 and 2008; earliest continuous chain production occurred in mid- to late August 1996, 1998, 2000, 2001 and 2004. Continuous chain production was in place by early to mid-September during all other years except for 1994 when it was delayed to early October.

Duration of chain production each year represented by back-to-back surveys was estimated using the age of primary length modes sampled during February–March surveys. Earliest termination of chain production appeared to occur in late November 2002 and December 1993, 1997, 1999 and 2000 (Fig. 11). In contrast, active chain released continued until at least mid- to late-February during 1996, 1997, 2002, 2004, 2005 and 2008. Based on these estimates, the duration of active chain production ranged between 73 and 187 days. The shortest period of chain production occurred during spring 1993, 1997 and 2002 (73–92 days) and the longest extended into summer of 1997, 2002 and 2005 (175–187 days). Based on leg 1 data, chain release also most likely continued into February 2006 and 2009 (Fig. 11). While the duration of chain production appeared to be prolonged after the 1998 regime shift (Martinson et al., 2008; Loeb et al., 2010) relative to the earlier portion of the data set (1994–1999, $N = 6$, mean = 125 ± 37 days; 2000–2008, $N = 7$, mean = 141 ± 44 days) the difference was not significant (ANOVA, $P > 0.05$). Primary length modes observed during all 29 AMLR surveys (Table 4) indicate peak aggregate production during November (34% of surveys), December (28%), January (14%) and February (24%).

3.6. *Salpa* abundance and demography in relation to ENSO

We examined the relationship between *S. thompsoni* and large-scale environmental conditions using the 1993–2009 data set. Unlike previous studies based on the 1980–2004 Elephant Island area data (Loeb et al., 2009, 2010), there was no significant correlation between salp abundance and sea ice extent the previous winter ($N = 15$, $T = -0.09$). However, abundance of total salps, aggregate and solitary stages and proportions of the solitary stage during January–March 1995–2009 surveys were significantly correlated with mean seasonal SOI and/or Nino3.4 values during the previous 2 years (Table 7, Fig. 12).

Kendall's Tau correlation tests (Table 7) indicate significant negative correlations between total salp abundance and the SOI during the previous 6–12 months (winter, fall and summer, $P < 0.05$) and a strong positive correlation with the Nino3.4 index the previous fall ($P < 0.001$). Abundance of both the aggregate and solitary stages shared significant positive correlations with the fall Nino3.4 index ($P \leq 0.01$); solitary stage abundance was also significantly correlated with the winter Nino3.4 index ($P < 0.05$). Interestingly, aggregate abundance exhibited a strong positive relationship with the SOI during summer 24 months earlier ($P < 0.01$) and solitary abundance was positively correlated with winter and fall SOI 18–21 months before ($P < 0.05$). Furthermore, elevated proportions of solitary stages were positively (negatively) correlated with SOI (Nino3.4) prevailing between fall and summer months 12–21 months

Table 7
Kendall's Tau correlation coefficients and significance levels (2-tailed) associated with mean abundance of *Salpa thompsoni* (total salps), the aggregate and solitary stages and proportions of total salps represented by the solitary stage during each survey leg, 1993–2009 relative to mean spring (October–December), winter (July–September), fall (April–June) and summer (January–March) SOI and Nino3.4 values lagged by 3–24 months. Significant lagged correlations and their associated probabilities indicated by bold type.

JFM	N	Season Months Lag	Spring OND 3	Winter JAS 6	Fall AMJ 9	Summer JFM 12	Spring OND 15	Winter JAS 18	Fall AMJ 21	Summer JFM 24
Total Salps	31	SOI	−0.21	−0.29 (0.02)	−0.30 (0.02)	−0.25 (0.046)	−0.02	0.04	0.07	0.10
	31	Nino3.4	0.19	0.13	0.45 (0.0004)	0.16	0.06	0.02	0.16	−0.06
Aggregate stage	26	SOI	−0.11	−0.15	−0.15	−0.17	0.12	0.14	0.25	0.36 (0.009)
	26	Nino3.4	0.11	0.13	0.40 (0.004)	0.15	0.08	0.10	−0.04	−0.24
Solitary stage	26	SOI	−0.20	−0.24	−0.21	−0.06	0.24	0.29 (0.03)	0.31 (0.02)	0.22
	26	Nino3.4	0.26	0.29 (0.04)	0.34 (0.01)	0.19	−0.03	−0.05	−0.22	−0.16
% Solitary stage	26	SOI	0.02	−0.03	0.10	0.27 (0.045)	0.32 (0.02)	0.34 (0.01)	0.28 (0.04)	−0.06
	26	Nino3.4	0.17	0.22	−0.08	−0.33 (0.02)	−0.35 (0.01)	−0.34 (0.01)	−0.32 (0.02)	0.02

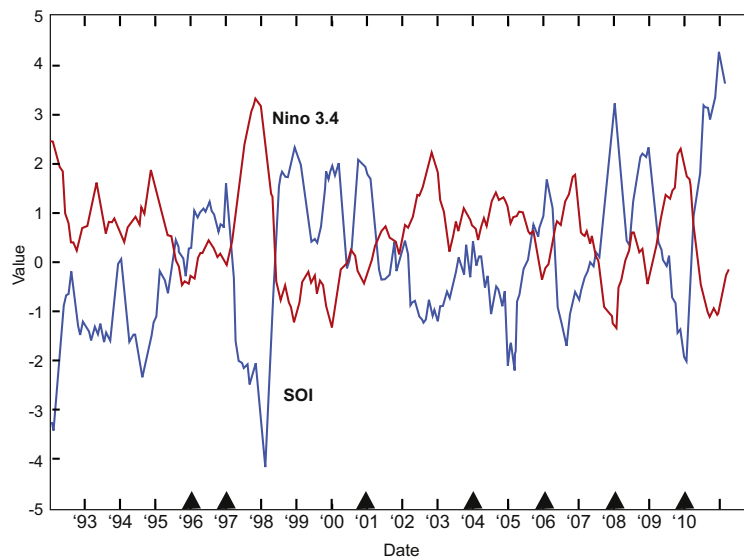


Fig. 12. Southern Oscillation Index (SOI) and Nino3.4 anomalies, 1992 to 2011, showing variations between atmospheric and oceanic conditions impacting the Antarctic Peninsula region over the study period. Diamonds indicate reversals between La Niña and El Niño events.

earlier ($P < 0.05$). These results strongly support the role of multi-year atmospheric-oceanic processes associated with ENSO underlying the population dynamics of *S. thompsoni*.

4. Discussion

4.1. Overview

Because of the role of salps in carbon cycling and their ability to undergo massive blooms, a basic understanding of their population dynamics, particularly with respect to climate variability, is essential for refining food web models. In the Southern Ocean, where *S. thompsoni* frequently is the numerical and biomass dominant zooplankton taxon, this information is critical to quantify alternate ecosystem pathways to those centered primarily on *E. superba* (Moline et al., 2004; Murphy et al., 2007). Few Southern Ocean data sets of necessary temporal coverage (e.g., >15 years, covering mul-

multiple ~5–7 year ENSO cycles), and with appropriate salp length and maturity stage information, exist to examine the complicated life history of *S. thompsoni* with respect to physical conditions that favor its reproductive success. This study builds on the work of Foxton (1966) and uses a 17 year, replicated spatial data set to examine the population dynamics of *S. thompsoni* and quantify interannual variability of abundance, carbon biomass, maturity stage composition and length–frequency characteristics. Changes in length–frequency characteristics between back-to-back summertime surveys, conducted over 8 years each, are used to establish growth rates of the two maturity stages. Intraseasonal and interannual variations in maturity stage composition and abundance are used to establish the time frame over which atmospheric-oceanic processes associated with ENSO provide optimal conditions leading to the development of massive salp blooms. We found that both aggregate and solitary stage production are enhanced during periods following reversal from La Niña to El Niño conditions in the Pacific basin (Fig. 12). Therefore, results of this

study have broad implications for our understanding of ecosystem dynamics in a generally perceived krill-centered food web (Murphy et al., 2007) and for ecosystem-based management of marine living resources in the Southern Ocean (Constable et al., 2000, 2003).

4.2. Growth rates

Growth rates of the aggregate and solitary stages of *S. thompsoni* have previously not been well established. Foxton (1966) was unable to conjecture on aggregate growth rates due to the patchiness and complex length–frequency distribution patterns of this stage in the Discovery samples. More recently, using aggregate length changes between January and March off the Adelie Coast, east Antarctica, Chiba et al. (1999) noted an increase of 11.6 mm over a 40–50 day period (0.23–0.29 mm per day), which corresponds to a ~7–9 mm growth rate over 30 days. However, Chiba et al. (1999) noted that this was extremely low compared to that of closely related temperate water species *S. fusiformis*, even when temperature differences were taken into consideration. Our estimated aggregate growth rate of 0.40 (± 0.05) mm day⁻¹, based on 87 length mode comparisons over eight field seasons, is the first derived for *S. thompsoni* utilizing a spatially and temporally comprehensive, multi-year data set. Our estimate is ~50% greater than that of Chiba et al. (1999) and yields a 0.4% increase in body length hour⁻¹ for the smallest (i.e., 4 mm) individuals, and 0.07% h⁻¹ increase of reproductive 25 mm individuals, at -1° to 2 °C ambient temperatures. These rates compare favorably with laboratory-based 1.3% and 0.3% h⁻¹ increases of the smallest (3–5 mm) and reproductive size (50 mm) individuals of subarctic species *Cyclosalpa bakeri* at 11 °C (Madin and Purcell, 1992) and 1.5–0.4% h⁻¹ increases of 2–22 mm *S. fusiformis* at 15 °C (Braconnot et al., 1988).

Based on a 0.4 mm day⁻¹ aggregate growth rate, the approximate timing of seasonal chain release and peaks of chain production between 1993 and 2009, presented in Fig. 11 and Table 4, are consistent with the seasonality described by Foxton (1966). Notably, these include: active chain production commencing in August and September; elevated production between October and March; and periods of peak production in November and February.

Foxton (1966) estimated that the overwintering solitary stage of *S. thompsoni* grew ~6–8 mm month⁻¹ based on length changes between March and September. Based on length changes between January and March, the overall solitary growth rate presented here, 0.23 \pm 0.04 mm day⁻¹, yields a 7 mm mean and range of 5.7–8.1 mm over a 30 day period. This growth rate is in accordance with Foxton's (1966) estimate.

Based on the growth rate estimates from this study, the life cycle of *S. thompsoni* (Fig. 3) averages 274 days, roughly 9 months, between initial aggregate chain release, solitary production and subsequent initiation of chain release. The timing of this life cycle is such that aggregates are released during spring and summer months, presumably when upper water column conditions are most likely to favor successful fertilization (Miller and Cosson, 1997) and offer optimal feeding conditions to fuel subsequent embryonic development (LeFèvre et al., 1998). A 2 month aggregate generation time span fits the narrowest window of summertime conditions supporting their successful fertilization and embryonic development. This time span also permits reproduction and survival of multiple chains released by each solitary during prolonged periods (e.g., extending from early spring to fall) should conditions be favorable. The slower solitary growth rate and 7.5 month generation time, compared to the aggregate, is appropriate for development at depth during fall and winter months when upper water column productivity is minimal. While the completion of one life cycle (i.e., initiation of chain production, subse-

quent solitary production, maturation and initiation of chain production) takes ~9 months, the typical maximum and extreme lengths of the aggregates and solitaries represented during January–March surveys indicate respective life spans of ~5–7 and ~15–24 months, respectively. The extended aggregate life span may provide prolonged incubation of the developing solitary. As noted above, an extended solitary life span permits multiple chain production.

The significant difference in solitary stage growth rates between 1997–2000 and 2001–2005 cannot be discounted as it coincided with a climate regime shift off the Antarctic Peninsula evidenced by increased ACC vs. Weddell Sea water influence after 1998 (Martinson et al., 2008; Loeb et al., 2010). The eastern portion of the AMLR study area, between Elephant, Clarence and Joinville Islands (Fig. 4a), is a major pathway of outflow from the clockwise Weddell Sea gyre and a region of rapid mixing and modification of waters from disparate sources (von Glydenfeldt et al., 2002; Thompson et al., 2009). Loeb et al. (2010) hypothesized that, during the earlier regime, abundant *S. thompsoni* were transported here from source waters northeast of the Weddell Sea. The presence of *S. thompsoni* in such high latitude waters (e.g., to 68°S) can be explained by poleward intrusions of warm CDW at depth, derived from the ACC (Pakhomov et al., 2002), which is consistent with an energized Weddell Sea gyre during that regime (Loeb et al., 2010). Additionally, Foxton (1966) reported that small solitaries collected at depth (>250 m) had a much slower growth rate than those within upper 100 m. Therefore, it is possible that solitary stages released within deep, warm water layers at high latitudes, and existing close to their “thermo-physiological limits” (Chiba et al., 1999; Pakhomov et al., 2002), would have depressed growth rates compared to those released within near surface waters more directly influenced by the ACC.

4.3. Reproductive success

It is often stated that under optimal conditions salps can rapidly undertake explosive population blooms, but this applies to lower latitude species which typically have life cycles of less than 6 weeks (Madin and Deibel, 1998). This is not true for *S. thompsoni* which, as demonstrated here, has a 9 month life cycle.

Daponte et al. (2001) remarked on observations by Heron and Benham (1984) that, for temperate water *T. democratica*, few immature solitaries appear when salps are sparse but are much more abundant when salps are dense. They conjectured that this was due to higher mating success in dense populations, since sperm are shed directly into the water and must be ingested by recently released aggregates in order for subsequent internal fertilization (Miller, 1984). Records of failed impregnation and dead embryos within *S. thompsoni* aggregates (Chiba et al., 1999; Daponte et al., 2001; Pakhomov et al., 2006, 2011) indicate the critical impacts of conditions supporting successful fertilization and subsequent growth and development of the embryo. However, our data show that, for *S. thompsoni*, elevated proportions of all solitary length/maturity stages in summer preceded population blooms during the subsequent one to two summers, suggesting that elevated production of both the aggregate and solitary stages (asexual and sexual reproduction) over at least two generations is required. Under this scenario, a sequence of optimal conditions must occur over all four seasons and span one or more years. These include (a) spring and summertime conditions favoring aggregate stage fertilization (e.g., aggregation and concentration; Miller and Cosson, 1997; Daponte et al., 2001), subsequent embryonic development (e.g., nutrition; Chiba et al., 1999) and solitary birth peaking in autumn; (b) suitable overwintering conditions for the solitary stage (e.g., nutrition, CDW derived from the ACC; Pakhomov et al., 2006, 2011) and (c) springtime conditions (ice

free water, particle concentrations; Pakhomov et al., 2002) favoring growth and multiple chain release by the solitaries.

4.4. ENSO and salp blooms

A more or less predictable sequence of environmental conditions across multi-year periods can be attributed to large-scale coupled atmospheric–oceanic processes such as those associated with ENSO forcing in the South Pacific and South Atlantic (Yuan, 2004; Loeb et al., 2009, 2010). This is supported by the significant correlations between salp abundance and demographic characteristics and SOI and Nino3.4 values lagged by 6–24 months (Table 7). Interannual and longer term variability in seasonal sea ice extent has been shown to be significantly correlated with salp abundance and krill recruitment success (Siegel and Loeb, 1995; Loeb et al., 1997; Atkinson et al., 2004). However, as noted by Loeb et al. (2010), these results were derived from older data sets (e.g., 1979–1996 for the Elephant Island area) that spanned a period of frequent El Niño events and radically reduced sea ice development off the Antarctic Peninsula. Using more recent data, including the 1999–2009 period characterized by increased influence of La Niña events and altered ocean–atmosphere–sea ice processes following the 1998 regime shift (Martinson et al., 2008; Stammerjohn et al., 2008; Loeb et al., 2010), SOI and Nino3.4 have replaced sea ice extent as the significant factors associated with krill recruitment success and salp abundance fluctuations in the Antarctic Peninsula region.

The nature of environmental conditions driven by ENSO forcing that favor population buildup leading to large summer blooms of *S. thompsoni* warrant further scrutiny. However, based on the shifts from positive to negative SOI (negative to positive Nino3.4) values (Table 7, Fig. 12) they appear to be initiated during the reversal from La Niña to El Niño conditions within the multiyear ENSO cycle.

While the AMLR data were derived from a limited geographic locale, the salp blooms noted here were not necessarily a localized phenomenon. Extremely large *S. thompsoni* concentrations monitored during the 2009 AMLR survey were also reported from the Palmer Peninsula, West Antarctic Peninsula, and Weddell Scotia Confluence south of South Georgia (Debbie Steinberg, NSF LTER, and Angus Atkinson, BAS, pers. comm.) and presumably were associated with the southern portion of the ACC (e.g., shoaling of CDW at its southernmost extent). Such widespread distributions of bloom conditions would be expected from basin-scale forcing by ENSO.

4.5. Long term salp abundance increase

The absence of any trend in the abundance of *S. thompsoni* in the 1993–2009 time series employed here could result from the limited temporal extent. As noted by Loeb et al. (2010), greatest changes in salp and krill abundance in region were associated with dramatic sea ice loss in the 1980s; since then their respective abundance fluctuations have largely been related to ENSO cycles. However, the longer term abundance increase of *S. thompsoni* within its southernmost distribution range reported by Atkinson et al. (2004) could, in part, be explained by the apparent trend for seasonally prolonged chain production in recent years (Fig. 11). The lack of significance in this trend, like that of abundance, might be due to the temporal coverage of the data set. While the onset of seasonal chain production (Fig. 11) does not appear to have changed from that reported by Foxton (1966), extended duration of chain production into autumn could be associated with delayed sea ice advance. Stammerjohn et al. (2008) reported substantially decreased duration of seasonal sea ice cover off the West Antarctic Peninsula between 1979–1991

and 1992–2004. This reduction was primarily due to a 25–35 day delay in the mean day of sea ice advance in autumn and, secondarily, to a 15–25 day delay in the mean day of retreat in spring. A 25–35 day delay in sea ice advance approximates half the aggregate generation time, the time during which sexual reproduction occurs and embryos begin to develop (Fig. 10). Therefore, an extended period of chain release would permit increased: (a) numbers of chains produced per solitary individual and (b) numbers of aggregates released per chain, since these increase with solitary size (Foxton, 1966). Thus there is a potential for substantially increased production of the critical overwintering solitaries in high latitude regions influenced by the ACC and undergoing diminishing sea ice.

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