Modelling the life cycle of *Salpa thompsoni*

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A B S T R A C T

Salpa thompsoni is an important grazer in the Southern Ocean. It is found from the Subtropical Convergence southward to the coastal Antarctic Seas but being most abundant in the Antarctic Polar Frontal Zone. Low temperatures appear to negatively affect their development, limiting their ability to occur in the krill dominated high Antarctic ecosystems. Yet reports indicate that with ocean warming *S. thompsoni* have experienced a southward shift in their distribution. As they are efficient filter feeders, this shift can result in large-scale changes in the Southern Ocean ecosystem by increasing competitive or predatory interactions with Antarctic krill. To explore salp bloom dynamics in the Southern Ocean a size-structured *S. thompsoni* population model was developed with growth, consumption, reproduction and mortality rates dependent on temperature and chlorophyll *a* conditions. The largest uncertainties in *S. thompsoni* population ecology are individual and population growth rates, with a recent study identifying the possibility that the life cycle could be much shorter than previously considered. Here we run a suite of hypothesis scenarios under various environmental conditions to determine the most appropriate growth rate. Temperature and chlorophyll *a* were sufficient drivers to recreate seasonal and interannual dynamics of salp populations at two locations. The most suitable growth model suggests that mean *S. thompsoni* growth rates are likely to be ~1 mm body length d^{-1}, 2-fold higher than previous calculations. *S. thompsoni* biomass was dependent on bud release time, with larger biomass years corresponding to bud release occurring during favorable environmental conditions; increasing the survival and growth of blastozooids and resulting in higher embryo release. This model confirms that it is necessary for growth and reproductive rates to be flexible in order for the salp population to adapt to varying environmental conditions and provides a framework that can examine how future salp populations might respond to climate change.

1. Introduction

Salps are highly efficient grazers that are ubiquitous throughout the world's oceans (Alldredge and Madin, 1982). They are capable of rapidly filtering particles up to a rate of 100 mL min^{-1} (Harbison and Gilmer, 1976) and their grazing pressure regionally can exceed the total daily primary production (Dubischar and Bathmann, 1997). Salps can efficiently re-package small particles into larger ones, either through fast sinking, carbon-rich faecal pellets (Bruland and Silver, 1981; Perissinotto and Pakhomov, 1998a) or salp carcasses (Henschke et al., 2013; Smith et al., 2014). As a result, the influence of salp swarms on the biogeochemical cycles are substantial, contributing 10-fold more

carbon to the seafloor than in areas without salp swarms (Fischer et al., 1988). However, this contribution is sporadic, and as the majority of studies are based on "potential" estimates there is uncertainty surrounding the total export flux produced by salps. A recent study suggests that recycling of salp faecal pellets in the epipelagic layer may be more common than previously believed, with only ~13% of produced pellets captured in sediment traps at 300 m (Iversen et al., 2017).

Salpa thompsoni is the most prominent pelagic tunicate in the Southern Ocean, found from the Subtropical Convergence southward to the coastal Antarctic Seas but being most abundant in the Antarctic Polar Frontal Zone (Foxton, 1966; Pakhomov et al., 2002; Loeb and Santora, 2012). In recent decades reports indicate that *S. thompsoni*

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have experienced a southward shift in their distribution, resulting in increased abundance in the traditionally krill dominated high Antarctic (Loeb et al., 1997; Chiba et al., 1998; Pakhomov et al., 2002; Atkinson et al., 2004), and possibly linked to a decline in Antarctic krill abundance (Atkinson et al., 2004). However, the ability of *S. thompsoni* to proliferate in the high Antarctic remains limited as low temperatures (< 1 °C) negatively affect their reproductive development (Casareto and Nemoto, 1986; Chiba et al., 1999; Pakhomov et al., 2011; Ono and Moteki, 2013).

Salp growth rates have been found to vary depending on environmental conditions such as temperature and food availability (Heron, 1972; Deibel, 1982; Heron and Benham, 1984), however, "optimal" conditions promoting maximum growth are still unknown.

Salpa thompsoni growth rates have only been estimated from cohort analysis of length-frequency distributions (Loeb and Santora, 2012; Pakhomov and Hunt, 2017). Loeb and Santora (2012) analyzed *S. thompsoni* length-frequency distributions across 17 years (1993–2009) of austral summer (January–March) surveys near the Antarctic Peninsula. From evaluating changes in length modes between median survey dates, their growth rate estimates for *S. thompsoni* ranged from 0.15–0.52 mm d^{-1} (0.3–4.6% d^{-1}), with a 9 month generation time (Loeb and Santora, 2012). These long generation times suggest that for large abundances of *S. thompsoni* to occur, favorable conditions must have occurred for one or more previous years. More recently, Pakhomov and Hunt (2017) performed an Eulerian study in the Antarctic Polar Front to also estimate growth rates from length-frequency distributions. Samples were of high temporal resolution, every 2–3 days over an 18 day period in the 2012 austral summer (Pakhomov and Hunt, 2017). Calculated growth rates were on average 2–3 fold higher than the Loeb and Santora (2012) estimates; 0.2–3.3 mm d^{-1} (3.7–20.7% d^{-1}), suggesting generation times could be as short as 3 months (Pakhomov and Hunt, 2017). These high growth rates were similar to preliminary data collected during late summer in the Antarctic Polar Front in 2004 (von Harbou, 2009).

The variations in *Salpa thompsoni* growth rates highlight some of the limitations of using cohort analysis to determine growth rates. Cohort analysis of length-frequency distributions assume that each sample is from the same population, that growth rates are constant between sampling periods and that growth rate estimates are representative of all size distributions. These assumptions may be difficult to meet for organisms such as salps because their patchy nature and tendency to swarm during mating aggregations or from physical turbulence (Graham et al., 2001) mean it can be hard to find and track a representative population, especially if sampling periods are weeks/ months apart. Yet as salps are difficult to culture in the laboratory (Raskoff et al., 2003), there is a lack of experimental data on salp growth rates and no experimental data for *S. thompsoni*.

Considering this uncertainty in *Salpa thompsoni* growth rates, our aim was to develop a population model in which we could determine the most appropriate growth relationship by simulating *S. thompsoni* populations under various environmental conditions. We can use population modelling to enhance our understanding of the existing cohort analysis datasets by understanding the demographic drivers that underlie patterns in the data. While there are other mechanisms that influence population dynamics such as mortality and reproductive timing, here we focus on growth rates, as the ability for salps to respond rapidly to environmental fluctuations is a key method for their swarming success. To determine the most appropriate growth rate relationship we ran the model under a suite of growth rate scenarios (hypotheses) and compared outcomes with observed patterns in *S. thompsoni* populations in the Southern Ocean. The scenarios were: Hypothesis 1 (H$_1$) – Loeb and Santora (2012) "slow" growth rates; Hypothesis 2 (H$_2$) - Pakhomov and Hunt (2017) "fast" growth rates; and Hypothesis 3 (H$_3$) – "Proportional" growth rates where energy for growth and reproduction are constant proportions of consumption.

2. Methods

2.1. Model description

A size-structured *Salpa thompsoni* population model was developed to explore salp bloom dynamics in the Southern Ocean. The model follows cohorts of individuals at a daily time step. Three life stages are modelled: female blastozooids, male blastozooids and oozoids (Fig. 1). Female blastozooids will grow, and once sexually mature, they will release one oozoid embryo. At the end of sexual reproduction, functional females develop testes, transition into males and continue to grow while actively fertilizing young female blastozooids. Oozoids will grow and store energy for reproduction, and once enough energy is available, they will release up to four chains of genetically identical female blastozooid buds. The model uses eight state variables to simulate the life cycle: the number (F_N, individuals (ind.) m^{-3}) and size (F_C, mg C) of female blastozooids, the number (M_N, ind. m^{-3}) and size (M_C, mg C) of male blastozooids, the number (O_N, ind. m^{-3}) and size (O_C, mg C) of oozoids and the amount of stored female (F_R, mg C) and oozoid (O_R, mg C) reproductive energy. Abundance and biomass (size) are tracked throughout the model to be consistent with observations. Temperature and chlorophyll *a* (a proxy for food abundance) have been shown to be important drivers of salp population dynamics (Heron, 1972; Deibel, 1982; Perissinotto and Pakhomov, 1998b; Kawaguchi et al., 2004; Henschke et al., 2014), and are included here as external drivers affecting growth, consumption, reproduction and mortality rates (Fig. 2).

2.1.1. Salp abundance

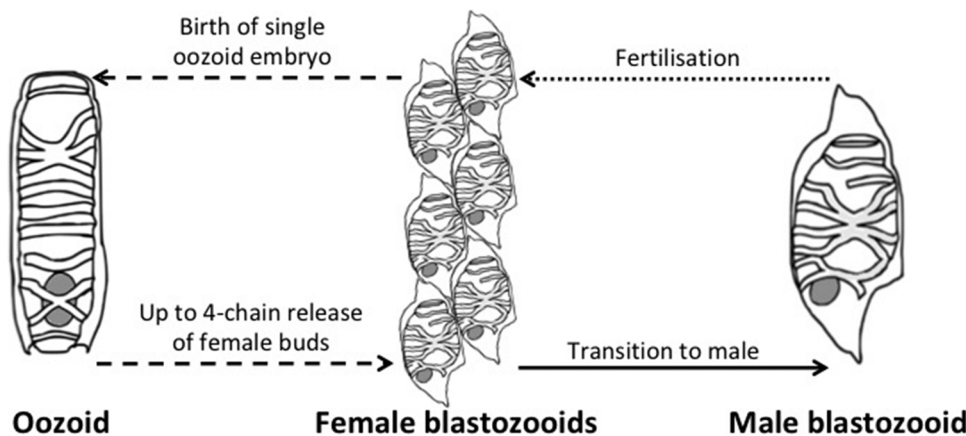The change of abundance of female blastozooids (F_N; ind. m^{-3}) in

Fig. 1. *Salpa thompsoni* life cycle. The typical salp life cycle involves the obligatory alternation between two life stages: the sexually reproducing blastozooids, and the asexually reproducing oozoids. In the blastozooid generation, the young blastozooid buds are female and are immediately fertilised upon release by older male blastozooids. These females grow a single internal embryo, which is the beginning of the oozoid generation. After releasing the oozoid embryo, the female blastozooids develop testes and function as male. The oozoid embryo grows to asexually produce up to four releases of genetically identical blastozooid buds. Dashed lines represent change of generation, the solid line represents growth and the dotted line represents external fertilisation.

Birth of single oozoid embryo

Fertilisation

Up to 4-chain release of female buds

Transition to male

Oozoid

Female blastozooids

Male blastozooid