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ORIGINAL PAPER

Demography and interannual variability of salp swarms (*Thalia democratica*)

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Abstract Swarms of the pelagic tunicate, *Thalia democratica,* form during spring, but the causes of the large interannual variability in the magnitude of salp swarms are unclear. Changes in asexual reproduction (buds per chain) of *T. democratica* populations in the coastal waters of south-east Australia (32–35°S) were observed in three austral springs (October 2008–2010). *T. democratica* abundance was significantly higher in 2008 (1,312 individuals m^{-3}) than 2009 and 2010 (210 and 92 individuals m^{-3}, respectively). There was a significant negative relationship (linear regression, $r^2 = 0.61$, $F_{1,22} = 33.83$, $P < 0.001$) between abundance and asexual reproduction. Similarly, relative growth rates declined with decreasing abundance. Generalised additive mixed modelling showed that *T. democratica* abundance was significantly positively related to preferred food >2 μm in size ($P < 0.05$) and negatively related to the proportion of non-salp zooplankton ($P < 0.001$). Salp swarm magnitude, growth, and asexual reproduction may depend on the abundance of larger phytoplankton (prymnesiophytes and diatoms) and competition with other zooplankton.

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Introduction

Dense swarms of salps, a pelagic tunicate, intermittently occur in oceans around the world as a result of favourable hydrographic conditions, such as intrusions of nutrient-rich water (Blackburn 1979; Heron and Benham 1984; Deibel and Paffenhofer 2009). Recent studies have related the patches of salps to meteorological and oceanographic data (Deibel and Paffenhofer 2009), and shown that cool, inner shelf water types promoted denser populations of the small salp, *Thalia democratica* (Henschke et al. 2011). It is still unknown, however, why the magnitude of salp swarms in the ocean can vary dramatically from year to year in the same location. A long-term 25-year study of *T. democratica* in the Mediterranean Sea found that interannual abundances vary over 3 orders of magnitude (Licandro et al. 2006). Similarly, a variability of 2–3 orders of magnitude in biomass was seen in consecutive spring seasons in the Californian Current (Lavaniegos and Ohman 2003).

Abundances of salps in swarms can often exceed 1,000 individuals (ind.) m^{-3} (Andersen 1998; Everett et al.

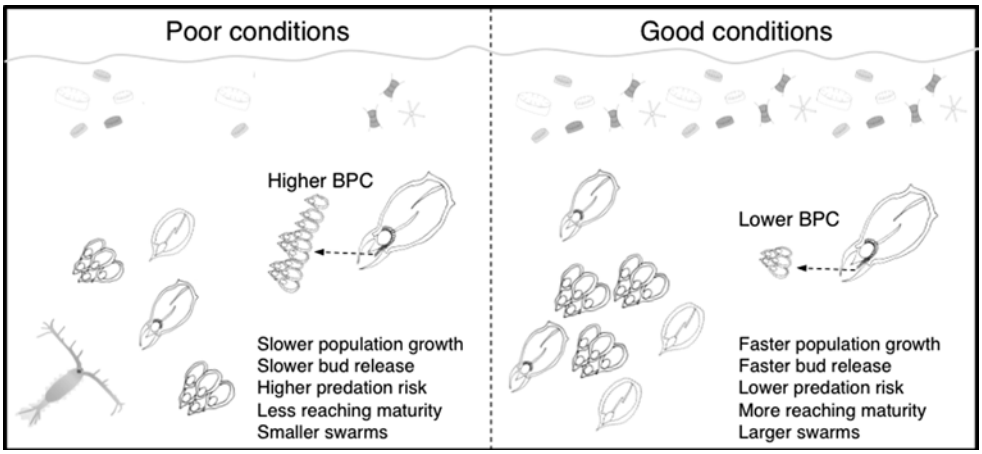

Fig. 1 Schematic diagram of Heron and Benham's (1985) overwintering theory. During poor conditions (*left pane*) such as winter, *T. democratica* oozoids will release longer chains of blastozooid buds (buds per chain; BPC). However, slow growth will result in young being exposed to predation and competition for longer, resulting in fewer reaching maturity and smaller swarm sizes. When conditions improve (*right pane*) in spring, oozoids will release shorter chains (lower BPC) more quickly that will grow rapidly and form larger swarms

2011; Henschke et al. 2011), constitute 99 % of the zooplankton biomass (Siegel and Harm 1996), and cover an area up to 100,000 km^2 (Madin et al. 2006). Salps are highly efficient filter-feeders, feeding on a wide size range of particles (0.1 μm to 1 mm), from bacteria to nauplii (Vargas and Madin 2004; Sutherland et al. 2010). The grazing pressure created by salp swarms can remove the daily primary production in an area (Dubischar and Bathmann 1997) and transfer this matter relatively efficiently to the sea floor in fast-sinking, carbon-rich faecal pellets (Bruland and Silver 1981). As a result, the influence of salp swarms on the biogeochemical cycle is substantial, playing a significant role in carbon fluxes (Andersen 1998; Henschke et al. 2013). Understanding the processes affecting the magnitude of salp swarms will aid understanding of their role in the biological carbon pump and support the development of reliable biogeochemical and ecosystem models.

The salp life cycle involves the alternation of aggregated sexual and solitary asexual reproduction to generate swarming (Alldredge and Madin 1982). Solitaries (oozoids) asexually produce a chain of genetically identical individuals (buds). These aggregate (blastozooid) buds are born female and immediately fertilised after release from the oozoid. Once they develop and release one embryo, blastozooids then develop testes and fertilise the next generation of recently released buds. The embryo is the start of the next oozoid generation (Heron and Benham 1985; Fig. 1 in Henschke et al. 2011). Although sexual reproduction only results in one offspring per parent, *T. democratica* oozoids can asexually produce 1–3 separate releases of 20–80 buds (Heron 1972). Combined with fast growth rates, this results in rapid population growth, as one oozoid individual can potentially produce 240 blastozooid offspring in a week (Heron 1972). Swarms of salps tend to be ephemeral, only lasting from 1 week up to 1 month (Deibel and Paffenhofer 2009). As this duration corresponds to generation times of *T. democratica* (Braconnot 1963; Deibel 1982), it suggests that one of the main drivers of swarm formation is asexual reproduction.

Thalia democratica regularly swarm after the spring phytoplankton bloom (Heron 1972; Deibel and Paffenhofer 2009), and it is likely that swarm magnitude may be more dependent upon phytoplankton composition and/or abundance than water types or predation. Similarly, Heron and Benham's (1985) theory of "overwintering" *T. democratica* populations suggest that asexual reproduction varies depending on environmental conditions (Fig. 1). In poorer conditions, oozoids grow slowly, nursing longer chains of buds. Due to slower growth rates, the more vulnerable smaller stages (Heron et al. 1988) will be exposed to predation for longer, resulting in a lower percentage of young reaching maturity and smaller swarm sizes overall. On the other hand, when conditions are more suitable, the oozoid individuals have faster growth rates, produce shorter chains of buds more rapidly, and successfully reach maturity (Heron and Benham 1985; Deibel and Lowen 2012). Hence, we suggest that asexual reproduction (buds per release) and population growth rates can be used as an indicator of nutritional status. Although "buds per release" may be a more accurate term as a measure of asexual reproduction, for the remainder of this manuscript, we use the term "buds per chain" to be consistent with the existing literature.

Here, we examine the magnitude and demography of *T. democratica* swarms during the austral spring (September–November) across 3 years. Our first aim was to examine the annual salp swarms of 3 research voyages (2008–2010) in the context of a zooplankton monitoring station (2002–2010) off Sydney. To examine swarm demographics, asexual reproduction and growth rate for each swarm was calculated. In order to have a comparable measure of growth rate across the three swarms, growth rate was calculated from formalin-fixed *T. democratica* samples using methods by Heron and Benham (1985). This calculation is based on the significant correlations between five life history stages and previously estimated growth rates (Heron and Benham 1984, 1985). Heron and Benham's (1985) growth calculation generally results in faster growth rates when compared with laboratory experiments (Deibel 1982; Le Borgne and Moll 1986). Our second aim therefore, was to assess the validity of Heron and Benham's (1985) growth calculation as either a direct or relative measure, by comparing with growth rate experiments conducted on live specimens from the same population. Our third aim was to identify links between environmental conditions, in particular the phytoplankton community composition and *T. democratica* swarm demographics (asexual reproduction and growth rate) across three consecutive spring seasons.

Methods

Long-term *Thalia democratica* sampling

Zooplankton were sampled monthly from January 2002 to December 2012 at the Port Hacking National Reference Station (NRS; 100 m deep) off Sydney, Australia (34°09′S, 151°15′E; Fig. 2). A 20-cm-diameter 100-μm mesh net was used to sample from 2002 to January 2009. Since February 2009, a larger 60-cm-diameter net has been used with the same mesh size. Nets were dropped at a rate of

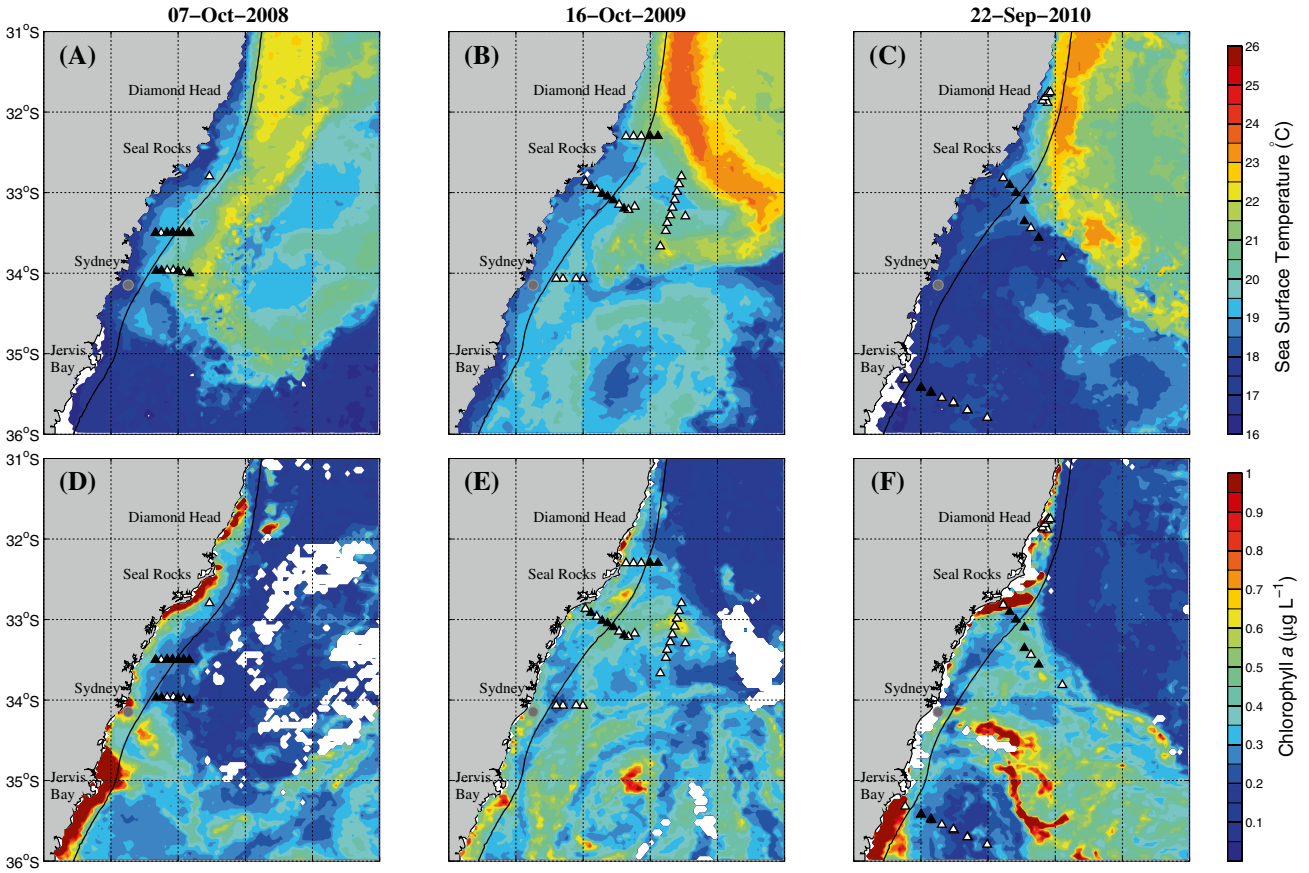

Fig. 2 Study area with satellite-derived sea surface temperature (°C; **a–c**) and chlorophyll *a* (μg L^{-1}; **d–f**) overlaid. Images best represent conditions occurring on the first day of oceanographic sampling across the 3 years (Table 1). Due to cloud cover, satellite data represent an 8-day composite of sea surface conditions ending with the date given. Zooplankton sampling locations are represented by *triangles*. *Black triangles* denote stations that were used for asexual reproduction analysis. *Grey circle* indicates location of the Port Hacking National Reference Station. *Black line* refers to 200 m isobath

1 ms^{-1} to 100 m below the surface using a drop net (Heron 1982). Samples were fixed in a 5 % formalin solution and analysed by the Plankton Ecology Laboratory, CSIRO. Data presented in this paper are single values from each haul ($N = 94$) but averaged for monthly analysis. Data are freely available via the Integrated Marine Observing System (IMOS) data portal: http://imos.aodn.org.au/.

Oceanographic sampling procedure

Three austral spring (September–November) voyages aboard the R.V. *Southern Surveyor* were undertaken off south-east Australia in the Tasman Sea in 2008, 2009, and 2010 (Table 1). The study area extended from Diamond Head in the north (31°30′S, 152°30′E) to Jervis Bay in the south (35°03′S, 150°43′E; Fig. 2). Samples were collected along transects from the inner shelf water type (Cresswell 1994; Henschke et al. 2011). Data included in this paper from 2008 were a random selection from inner shelf stations previously determined by Henschke et al. (2011). These locations were chosen with the aid of daily Moderate Resolution Imaging Spectroradiometer (MODIS) and Advanced Very High Resolution Radiometer (AVHRR) satellite imagery during the cruise. Transects had 5–12 equidistant stations. At stations along each sampling transect, a Seabird SBE911-plus Conductivity–Temperature–Depth (CTD) recorder equipped with an AquaTracker Mk3 fluorometer (Chelsea, UK) was used to record salinity, temperature, and fluorescence, respectively.

To investigate the vertical distribution of the phytoplankton community (using chlorophyll *a* and accessory pigments) across the 3 years, water was collected from the surface and the depth of the chlorophyll *a* maximum (as determined by the downcast fluorescence profile), and four other depths (i.e. nominally surface, 10, 25, 50, 75, and 100 m). A minimum volume of 2.2 L was filtered under low vacuum (e.g. ≤100 mm Hg) onto 25 mm GF/F filters in low light (<10 μmol photons m^{-2} s^{-1}). Filters were folded in half, blotted dry on absorbent paper, placed into screw-capped cryovials, and stored in liquid nitrogen until pigment analysis in the laboratory.

Water for chlorophyll *a* and accessory pigment analyses in 2010 was opportunistically sampled a fortnight after

Table 1 Hydrographic and zooplankton characteristics across the 3 years

	2008	2009	2010
Sampling date	10/10/08–20/10/08	16/10/09–27/10/09	22/09/10–05/10/10[a]
Hydrographic conditions (mean ± SD)			
N	15	29	25
Temperature (°C)	19.25 ± 0.96 (18.24–21.45)	19.45 ± 0.88 (18.28–21.84)	18.29 ± 0.89 (17.31–20.17)
Salinity	35.54 ± 0.03 (35.46–35.57)	35.51 ± 0.04 (35.43–35.57)	35.55 ± 0.04 (35.48–35.60)
N	4	12	17
Chlorophyll *a* (μg L^{-1})	0.74 ± 0.38 (0.40–1.22)	0.70 ± 0.18 (0.42–0.88)	0.45 ± 0.63 (0.08–2.44)
Zooplankton abundance (mean ± SD)			
N	14	27	24
Thalia democratica	1312.3 ± 545.0 (679.1–2,352.1)	210.2 ± 264.9 (0.6–1,113.6)	91.9 ± 118.7 (0–423.3)
Crustaceans	251.2 ± 170.8	399.3 ± 239.6	3,136.8 ± 4,705.7
Doliolids	45.4 ± 50.8	36.2 ± 91.9	304.5 ± 439.7
Larvaceans	31.4 ± 41.1	55.8 ± 57.1	3,441.3 ± 4,674.5
Chaetognaths	3.0 ± 3.1	8.9 ± 6.0	89.0 ± 64.4
Other	41.2 ± 25.0	84.0 ± 47.4	229.8 ± 154.5
Total non-salp zooplankton	372 ± 238	584 ± 298	7,201 ± 9,311
Thalia democratica life history characteristics			
N	10	7	7
Asexual reproduction (BPC)	36.08 ± 4.75 (31.8–48)	45.68 ± 7.48 (36.4–60)	53.15 ± 4.12 (47.9–58.5)
Blastozooid : Oozoid	11.2 ± 6.1 (5.5–26)	9.5 ± 3.9 (6.1–15.9)	8.8 ± 4.8 (4.5–15.3)
Relative growth index (% length h^{-1})	16.5 ± 3.2 (8.2–22.6)	14.9 ± 2.1 (12.3–17.6)	11.5 ± 3.8 (6.4–17.5)
r_{max} (day^{-1})	2.8 ± 0.5 (1.4–3.2)	2.7 ± 0.3 (2.2–3.1)	2.1 ± 0.7 (1.2–3.2)
N	31	24	19
Proportion of mature blastozooids (%)	13.51 ± 8.69 (0–41.2)	11.62 ± 8.42 (0.8–32.8)	5.55 ± 7.76 (0–26.6)

Inner shelf water characteristics are depth averaged over the top 50 m of the water column. Values are mean ± SD. Values in parentheses are ranges. Proportion of mature blastozooids is based on the percentage of population that is greater than 4 mm in length. *N* number of stations

[a] Second voyage for phytoplankton collection conducted 14/10/10–31/10/10

zooplankton sampling on a second voyage as the required phytoplankton expertise was not available during the salp sampling voyage. From the inspection of MODIS satellite imagery, there were similar oceanographic conditions between the two voyages in 2010, as Tasman Sea water still dominated the region with the EAC separation remaining around 33°S. This was later confirmed when comparing mean values for depth-integrated fluorescence across the two voyages (ANOVA, $F_{(1,69)} = 0.81$, $P = 0.37$). Phytoplankton assemblages sampled separately during 2010 at the Port Hacking NRS were dominated by prymnesiophytes in both September and October, and did not differ significantly between the 2 months (Paired t test, $t_{38} = 1.24$, $P = 0.22$; Data freely available from IMOS, http://imos.aodn.org.au/). As the hydrographic characteristics of the NRS have been shown to significantly correlate to inner shelf water in the area (Oke and Sakov 2012), we have shown statistically that phytoplankton assemblages in 2010 did not differ during the 2-week delay between zooplankton and phytoplankton samplings.

Pigment analyses

Phytoplankton pigment concentrations were estimated using high-performance liquid chromatography (HPLC) using procedures outlined in Doblin et al. (2011). HPLC analysis has the advantage of including all members of photosynthetic assemblages >0.7 μm (cell counts with a microscope typically resolve species >10 μm in diameter). The HPLC system was calibrated using phytoplankton reference cultures (Australian National Algae Culture Collection) with known pigment composition (Mantoura and Llewellyn 1983; Barlow et al. 1993; Jeffrey et al. 1997).

The approach of Uitz et al. (2008) was used to assess the taxonomic community composition of phytoplankton and yield information about its size structure. While this method may be subject to error because pigments are shared between different phytoplankton groups, or some groups may be spread across different sizes, this approach yields useful information, e.g. pico-, nano-, and microphytoplankton mainly include diatoms, prymnesiophytes (coccolithophorids), and prokaryotes, respectively.

Shipboard zooplankton sampling

At each CTD station, two replicate vertical hauls of a N70 net (Kemp and Hardy 1929) were made to 50 m for the collection of zooplankton. Modified from the original silk design, the 70-cm-diameter N70 net had 3 sections of differing mesh sizes: a 53-cm-long, 4-mm mesh section near the mouth; a 97-cm-long, 400-μm mesh section in the middle; and a 135-cm-long, 225-μm mesh section near the cod end. Samples from each net haul were concentrated to 100 mL in a 5 % formalin solution using a 200-μm sieve. In the laboratory, two replicate 1 mL subsamples were taken with a wide-mouth pipette from each net sample and examined in a Bogorov tray. Organisms were classified into groups commonly known to occur in the Tasman Sea: salps, doliolids, crustaceans, larvaceans, and chaetognaths (Thompson and Kesteven 1942). Other zooplankton identified in low numbers include molluscs, cnidarians, ctenophores, and annelids. Total length of the first 60 *T. democratica* individuals within each net haul sample was measured as by Foxton (1966), from the oral opening to the posterior ridge of the gut.

Shipboard growth experiments

In 2009, an extra vertical haul was undertaken at three sites (Table 2) for the collection of live *T. democratica* individuals for growth experiments. Mature oozoid *T. democratica* were removed from the cod end of the net and carefully transferred to a large (50-L) tank filled with site water taken from the surface depth. Salps were acclimatised overnight in a constant temperature room, with a 16/8 h light/dark cycle. The constant temperature room was maintained at the ambient temperature of the mixed layer (Table 2).

Lights were turned on at 0400 hours, preceding twilight, and oozoids bearing unreleased chains were transferred to individual 2-L tanks. Tanks were randomly allocated to three collection times, corresponding to how long the buds were left in the tanks to grow out following their release from the oozoid: T0 (buds collected immediately after release), T4 (buds collected 4 h after release), and T8 (buds collected 8 h after release) (Table 2). Salps were continually

Table 2 Stations for blastozooid growth experiments in October 2009

Experiment	N	Date of collection	Location	Ambient temperature (°C)	Growth rate (% length h^{-1})
1	12 (4,4,4)	19, 16:15 hours	33.30°S 154.35°E	20	2.32
2	19 (8,6,6)	20, 15:30 hours	33.25°S 152.67°E	21.5	1.83
3	26 (10,8,8)	21, 17:15 hours	33.20°S 152.61°E	20.5	2.20

Time is in Australia Eastern Standard time. N number of stations. Values in parentheses represent number of tanks allocated to each collection time: T0, T4, and T8, respectively

observed for the point of bud release and the time of release was recorded for each individual. To reduce the risk of mortality, water was gently mixed if salps became stuck on the surface due to surface tension (Heron 1972).

Blastozooid buds experience sudden increases in length as they are being born, which may alter calculated growth rates (Heron 1972), but all chains in this study were collected after being fully released by the parent to eliminate any birthing effect. Once buds were successfully released, the oozoid was removed from the tank and fixed in 5 % formalin, followed by the buds in the T0 group. Buds that were not fully released from their oozoid parent were removed from the experiment and not included in the data analysis. Buds from the T4 and T8 groups were subsequently collected after 4 and 8 h, respectively, and fixed in 5 % formalin solution. After collection, total lengths of buds and their oozoid parents were measured to estimate growth rates.

Thalia democratica demographic analyses

Stations for asexual reproduction analysis were chosen randomly from within inner shelf waters sampled during research voyages and ranged from 7 (2009, 2010) to 10 (2008) CTD stations across the 3 years. Asexual reproduction was measured by quantifying the number of buds produced from the oldest fully developed chain (buds per chain, BPC) of an oozoid individual. A chain was only considered fully developed if it was clearly distinguished from the stolon (Fig. 3). This approach reduced the potential error associated with a young chain having not yet finished segmenting at the time of capture. Asexual reproduction of 20 individuals was measured from each sample. Where 20 oozoid individuals could not be found, the maximum number within the sample was used (minimum = 4).

The relative growth index (RGI; % length h^{-1}) across the 3 years was calculated using life history stages of fixed salps (Heron and Benham 1985):

$$\mathrm{RGI} = 0.576 - 0.0876\ \ln(\mathrm{BPC}) - 0.0211\ \ln(\mathrm{OP}) \quad (1)$$

where BPC = buds per chain (asexual reproduction), OP = offspring-to-parent ratio (i.e. blastozooid to mature oozoid).

The standard error for Heron and Benham's (1985) growth index estimates ranged from 0.67 to 0.78 % length h^{-1}. This growth rate estimation was based on significant correlations that they found between five life history stages and previously estimated growth rates (Heron and Benham 1984, 1985). As these life history stages are not affected by shrinking as a result of fixing, this equation is robust for use after long periods of fixing (Heron and Benham 1985).

Lifetime fitness (r_{max} day^{-1}) was calculated using the growth index (Eq. 1) and asexual reproduction (BPC).

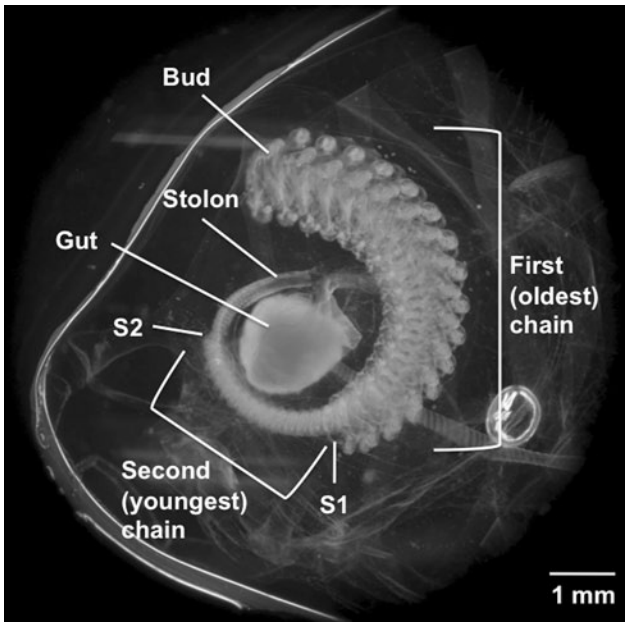

Fig. 3 Three chains of *T. democratica* buds in an oozoid individual. Buds in first and second chains are clearly segmented and distinguished from other chains (S1: first separation; S2: second separation). Buds from the third chain are still segmenting along the stolon. Only the first chain was considered for asexual reproduction analysis

Lifetime fitness refers to the maximum intrinsic rate of natural increase and is commonly used as a measure of adaption to different environmental conditions (Deibel and Lowen 2012). As a result, increasing lifetime fitness reflects decreasing population turnover rate. The following equation from Troedsson et al. (2002) was used

$$r_{\max} = \frac{\ln b}{T} \quad (2)$$

where b = lifetime egg production (BPC × 2.5) and T = generation time in days.

Lifetime egg production was calculated assuming that the number of cohorts produced by each oozoid was 2.5, the median of most commonly observed number of chains released (Deibel and Lowen 2012). Generation time was calculated as the time taken to complete one generation, assuming a standard maximum length of 15 mm for both blastozooid and oozoid individuals (Thompson 1948) and using the calculated growth index (Eq. 1).

Data analyses

An unbalanced one-way analysis of variance (ANOVA) was used to test the null hypothesis of no significant difference in each hydrographic condition (temperature, salinity, and chlorophyll *a*) across the three ship-based sampling years (fixed factor, $N = 3$). If the hydrographic data were

not normally distributed within each year, a Mood's median test was undertaken to test the null hypothesis that the median values of each variable did not differ significantly across the years (fixed factor, $N = 3$).

An unbalanced two-way ANOVA was used to test the null hypothesis of no significant difference in *T. democratica* abundance across years (fixed factor, $N = 9$) and seasons (fixed factor, $N = 4$) from the long-term NRS data. Unbalanced one-way ANOVAs were used to test the null hypotheses of no significant difference in oceanographic *T. democratica* abundance, asexual reproduction, and abundance of non-salp zooplankton among years (fixed factor, $N = 3$). Tukey's analysis was used for a posteriori pair-wise comparisons between factor levels for all ANOVAs. Regression analyses were used to examine the relationship between *T. democratica* abundance and asexual reproduction ($N = 27$). An analysis of covariance (ANCOVA) was used to examine the relationship between growth rate and asexual reproduction. The two different growth methods, Heron and Benham's calculation and the laboratory experiments, were included as covariates. Where necessary, data were log-transformed to improve the assumptions of normality assumption and homogeneity of variance, and to reduce the effect of outliers. All parametric tests were performed in R version 2.15.2 (R Development Core Team 2006).

Interannual variation in oceanographic phytoplankton assemblages was analysed using multivariate techniques. Bray–Curtis similarity matrices, based on log-transformed data, were constructed for both the phytoplankton community proxies (prymnesiophytes, diatoms, and prokaryotes) as well as the size proxies (pico-, nano-, and microphytoplankton). Principal coordinates analysis (PCO) was undertaken on these matrices to highlight relationships between phytoplankton communities across years. All multivariate nonparametric analyses were performed with PRIMER, version 6 (Clarke and Warwick 2001; Clarke et al. 2008).

To examine the links between *T. democratica* swarm magnitude and environmental conditions, the relationship between the abundance of *T. democratica* and environmental variables was analysed using a nonlinear generalised additive mixed-effects model (GAMM) (Hastie and Tibshirani 1990; Zuur et al. 2009). GAMMs extend traditional linear modelling by containing both random and fixed effects and applies a spline function to nonlinear explanatory variables (Hastie and Tibshirani 1990). A spline function creates a smoothed curve by sectioning the data into two or more segments and fitting polynomial curves to each segment (Zuur et al. 2009).

Prior to analysis, possible outliers or collinearity were identified through graphical analysis (boxplots and pair-wise scatter plots). No outliers were identified. Phytoplankton size classes were considered for the model instead of species composition as *T. democratica* are opportunistic filter-feeders whose retention efficiency is only limited by size (Vargas and Madin 2004). Food quality was grouped into two categories, preferred and non-preferred. Preferred included phytoplankton >2 μm (i.e. nano- and microplankton) as *T. democratica* retention efficiency for these particles ranges from 80 to 100 % (Vargas and Madin 2004). Non-preferred included picoplankton (<2 μm) as retention efficiency on these particles is only 40–50 % (Vargas and Madin 2004). As collinearity was observed between preferred and non-preferred food, preferred food was used as the main indicator of food quality. In addition to the preferred food, the other explanatory variables that were used in the original model were temperature, $\log_{10}$-chlorophyll *a,* and proportion of non-salp zooplankton. Year was included as a random variable. As the relationship between salp abundance and proportion of non-salp zooplankton was non-independent, it was at risk of producing a spurious correlation (Brett 2004). To determine whether a spurious correlation did exist, the procedure outlined by Brett (2004) was used, where the statistical significance of the correlation coefficient can be determined through Monte Carlo simulations. We randomly resampled the variables: salp abundance, total zooplankton abundance, and non-salp zooplankton abundance using the same sample size as the original data ($N = 36$) and distribution pattern (mean and standard deviation). This was run 1,000 times, and for each 1,000 random sets, proportion of non-salp zooplankton was recalculated using the random sets of non-salp zooplankton abundance and total zooplankton abundance. All sets of salp abundance were then correlated with all sets of proportion of non-salp zooplankton, resulting in 1,000 Pearson's correlation coefficients that were all spurious. The mean Pearson's correlation coefficient from these spurious data was then compared with the correlation coefficient of the original data to test the null hypothesis of no significant difference from the spurious data.

A smoothing function was used only for the proportion of non-salp zooplankton, as all other explanatory variables had a linear relationship with $\log_{10}$-transformed salp abundance. Backward stepwise elimination was used to select significant parameters, and the most parsimonious model was chosen by comparing Akaike's information criterion (AIC) across models. An analysis of the model residuals suggested that the model was robust. All analyses were performed using the mixed generalised additive model package "mgcv" in R (Wood 2006) available at: cran.r-project.org. Modelling was performed in R version. 2.15.2 (R Development Core Team 2006).

Results

Long-term *Thalia democratica* abundance

The long-term (2002–2010) abundance (ind. m^{-3}, mean ± SD) of *T. democratica* at Port Hacking was 45.81 ± 140.40 ind. m^{-3} ($N = 93$; Fig. 4a). There was no significant difference in abundances across years (ANOVA, $F_{(8,59)} = 0.94$, $P = 0.49$); however, populations were significantly more abundant during the austral spring (September–November) when compared to autumn and winter (ANOVA, $F_{(3,59)} = 2.91$, $P = 0.042$; Fig. 4c). *T. democratica* abundance was generally low during most of the year and peaked in abundance in September (195.55 ± 325.54 ind. m^{-3}, $N = 8$) and October (233.10 ± 299.28 ind. m^{-3}, $N = 6$; Fig. 4a) during the spring. *T. democratica* were also present more frequently in samples between September and October (Fig. 4b). Interestingly, following peak abundances and the presence of salps in September and October, November recorded the lowest presence of *T. democratica* in samples and mean abundances were an order of magnitude lower than previous months (Fig. 4a, b). In the months of our spring voyages, abundances of *T. democratica* were 637, 120, and 148 ind. m^{-3} (2008–2010, respectively; single tow values).

Hydrographic properties during the sampling period

The regional oceanography varied dramatically across the 3 years (Fig. 2). During 2008, the core of the East Australia Current (EAC) was 23 °C and had penetrated as far south as Sydney (34°S), with a strong eastward retroflection. During sampling, there was strong persistent upwelling off the coast at Seal Rocks (32°27′S). In 2009,

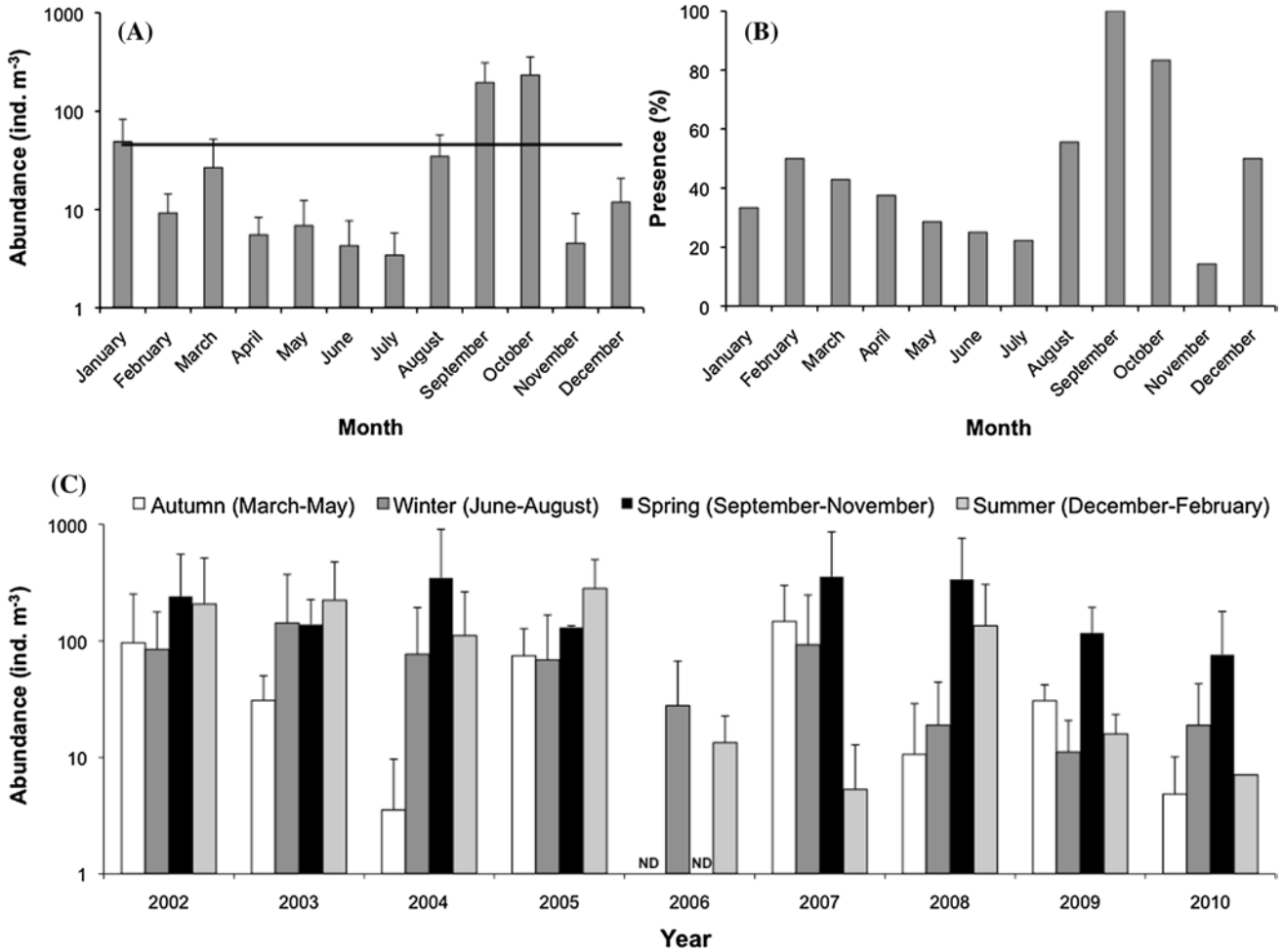

Fig. 4 **a** Mean (+SD) monthly abundance (ind. m^{-3}) for *T. democratica* at Port Hacking from 2002 to 2011. *Black line* represents long-term mean. *Scale* is $\log_{10}$-transformed. **b** Proportion of non-zero *T. democratica* hauls per month from 2002 to 2011. **c** Seasonal abundances (ind. m^{-3}) of *T. democratica* from 2002 to 2011. *ND* no data. *Scale* is $\log_{10}$-transformed

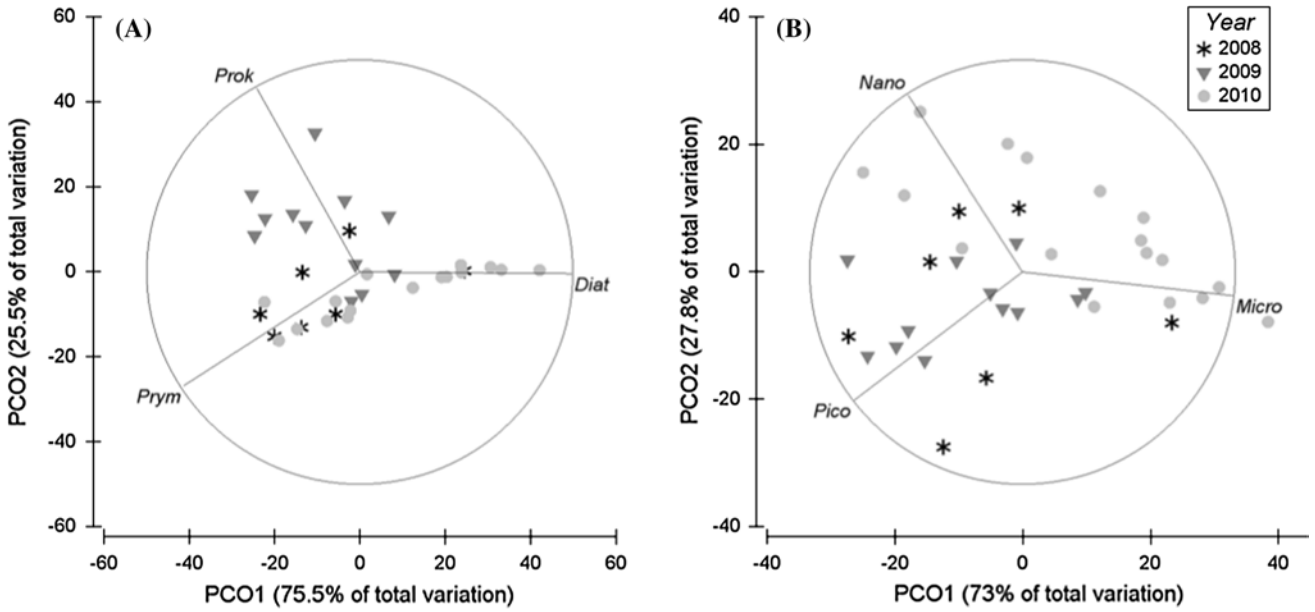

Fig. 5 Ordination of phytoplankton community structure using principal coordinates analysis, with year superimposed. Vectors overlaid are multiple correlations of **a** phytoplankton species groupings: diatoms (Diat), prymnesiophytes (Prym), and prokaryotes (Prok), and **b** phytoplankton size structure: picoplankton <2 μm (Pico), nanoplankton 2–20 μm (Nano), and microplankton >20 μm (Micro)

the EAC dominated the shelf off Sydney the month prior to sampling, but during sampling, a strong separation of the EAC from the Australian coast had formed at 32°S, with an average temperature of 23 °C. In 2010, the EAC (22 °C) had separated from the coast at 33°S and Tasman Sea water dominated the region. In both 2009 and 2010, a large cyclonic eddy was evident off the coast at 33°S and upwelling off Seal Rocks was not observed in either year during our sampling.

Hydrographic properties for inner shelf water (surface to 50 m) varied across the 3 years. In 2009, inner shelf water was less saline than in 2008 and 2010 (Table 1). Inner shelf water in 2010 was significantly cooler (ANOVA, $F_{(2,21)} = 7.52$, $P = 0.003$) and mean (±SD) chlorophyll *a* concentration was lower (0.45 ± 0.63 μg m^{-3}, median = 0.23 μg m^{-3}, $N = 17$) than 2008 and 2009 (0.74 ± 0.38 μg m^{-3}, median = 0.66 μg m^{-3}, $N = 4$, and 0.70 ± 0.18 μg m^{-3}, median = 0.77 μg m^{-3}, $N = 12$). Mood's median test confirmed that chlorophyll *a* levels were significantly lower in 2010 (chi-square test, $\chi^2_2 = 0.435$, $P = 0.001$, $N = 33$). HPLC analysis identified that the phytoplankton communities in the inner shelf water differed across the 3 years. PCO analysis on pigments identified that prymnesiophytes (containing 19′ hexanoyloxyfucoxanthin) dominated the phytoplankton community in 2008, prokaryotic picoplankton (containing zeaxanthin and divinyl-Chl-*a*) in 2009, and there was a mix of both prymnesiophytes and microplankton diatoms in 2010 (Fig. 5a, b).

Thalia democratica life history characteristics from ocean voyages

Thalia democratica was the dominant salp species sampled across the voyages; however, at a few stations, *Salpa fusiformis, T. orientalis,* and *Thetys vagina* occurred in low abundances (<5 ind. m^{-3}). *T. democratica* abundance varied significantly across years. Mean abundances (±SD) of *T. democratica* decreased significantly from 1,312.3 ± 545.0 ind. m^{-3} ($N = 14$) in 2008 to 210.2 ± 264.9 ind. m^{-3} ($N = 27$) in 2009 and were lowest in 2010 (91.9 ± 118.7 ind. m^{-3}, $N = 24$; ANOVA, $F_{(2,62)} = 76.9$, $P < 0.001$; Table 1, Fig. 6a).

The proportion of blastozooids reaching maturity were significantly lower in 2010 (5.55 ± 7.76, $N = 19$) than 2008 (13.51 ± 8.69, $N = 31$) and 2009 (11.62 ± 8.42, $N = 24$; ANOVA, $F_{(2,71)} = 5.47$, $P = 0.006$; Table 1). Although the blastozooid-to-oozoid ratio decreased throughout the years, this trend was non-significant (ANOVA, $F_{(2,21)} = 0.49$, $P = 0.62$).

Asexual reproduction (BPC) varied across years, significantly increasing each year from 2008 to 2010 (ANOVA, $F_{(2,23)} = 20.18$, $P < 0.001$; Fig. 6b). The relative growth index was significantly higher in 2008 (16.5 ± 3.2 % length h^{-1}, $N = 10$) than in 2010 (11.5 ± 3.8 % length h^{-1}, $N = 7$; ANOVA, $F_{2,21} = 5.43$, $P = 0.013$; Table 1). Lifetime fitness rates also declined across the years, from 2.7 to 2.8 day^{-1} in 2008 and 2009 to 2.1 d^{-1} in 2010 (Table 1); however, this trend was not significant (ANOVA,

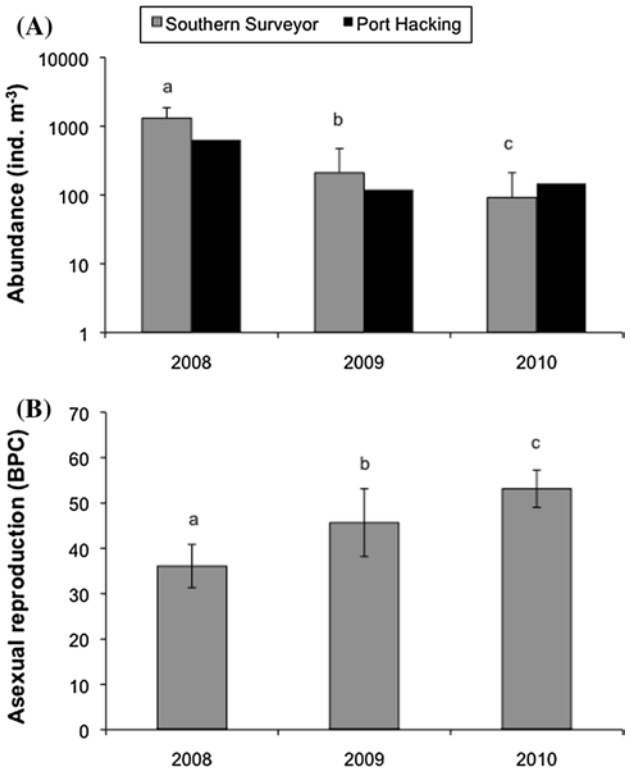

Fig. 6 **a** Mean (±SD) *T. democratica* abundance across 3 years of sampling (*Southern Surveyor* voyages) and for corresponding Port Hacking NRS hauls. **b** Mean (±SD) asexual reproduction (buds per chain) across the 3 years from *Southern Surveyor* voyages. *Letters* denote significant differences at $P < 0.05$ (ANOVA)

$F_{(2,21)} = 3.41$, $P = 0.052$). Regression analysis identified a significant negative relationship between *T. democratica* abundance and asexual reproduction (linear regression, $r^2 = 0.61$, $F_{1,22} = 33.83$, $P < 0.001$; Fig. 7).

Zooplankton community composition

In 2008 and 2009, mean (±SD) abundances of zooplankton excluding salps were 372 ± 238 ($N = 14$) and 584 ± 298 ind. m^{-3} ($N = 27$), respectively (Table 1). Copepods were the dominant group, comprising ~70 % of the non-salp fraction of zooplankton. Non-salp zooplankton were significantly more abundant in 2010 than 2008 and 2009, with a mean abundance of 7,201 ± 9,311 ind. m^{-3}, $N = 24$ (ANOVA, $F_{(2,62)} = 12.34$, $P < 0.001$). The non-salp zooplankton community composition also shifted, with copepods and larvaceans constituting ~90 % of the total zooplankton abundance in 2010.

Laboratory growth experiments

Blastozooid chains were released between 0330 and 0700 hours AEST, with 85 % of all chains released at

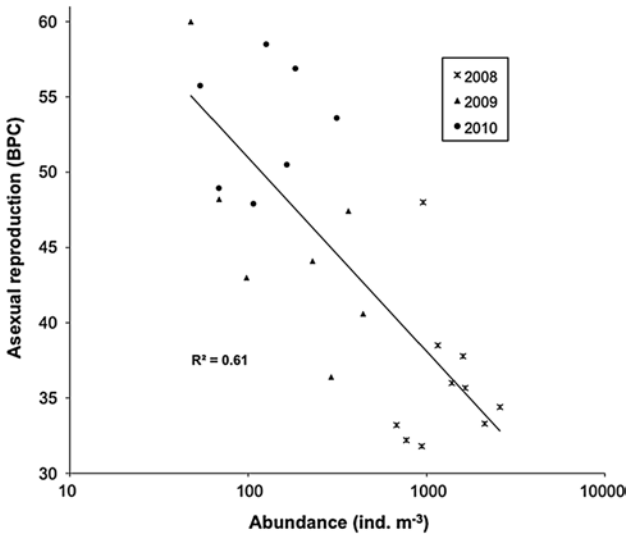

Fig. 7 Scatter plot showing relationship between $\log_{10}$-transformed *T. democratica* abundance and asexual reproduction (buds per chain; linear regression, $r^2 = 0.61$, $F_{1,22} = 33.83$, $P < 0.001$)

0530 hours regardless of time of capture. Experimental growth rates ranged from 1.83 to 2.32 % length h^{-1} (Table 2). Growth rates did not vary significantly during the two time periods, with initial growth rates (0–4 h) of 2.82 % length h^{-1}, being similar to later growth rates (4–8 h) of 2.12 % length h^{-1}. Experimental growth rates were significantly lower (2.12 ± 0.26, $N = 3$; ANOVA, $F_{(1,8)} = 101.84$, $P < 0.001$) than the relative growth index for the corresponding 2009 spring voyage (14.9 ± 2.1, $N = 7$). There was no significant difference between the mean (±SD) asexual reproduction (BPC) calculated from the experiments (42.35 ± 10.43, $N = 54$) and the mean asexual reproduction calculated from the 2009 voyage (45.68 ± 7.48, $N = 7$; ANOVA, $F_{(1,59)} = 0.66$, $P = 0.42$). There was no significant interaction between method of growth calculation (growth experiment or growth index) and growth rate (ANCOVA, $F_{(1,23)} = 0.25$, $P = 0.63$); however, there was a significant main effect for both factors (growth experiment, $F_{(1,23)} = 45.06$, $P < 0.001$ and growth index, $F_{(1,23)} = 4.97$, $P = 0.04$). This suggests that the slope of regression between growth rate and asexual reproduction was similar for both growth methods. Lifetime fitness values calculated from these laboratory-determined growth rates found mean (±SD) values of 0.38 ± 0.01 ($N = 7$), significantly lower than values calculated with the growth index (ANOVA, $F_{1,12} = 318.39$, $P < 0.001$).

Relationship between *Thalia democratica* abundance and the environment

Generalised additive mixed modelling (GAMM) identified a significant relationship between *T. democratica* and select

Table 3 Synopsis of the final additive mixed modelling analysis

Parametric coefficients					Smooth term			
	Estimate	Standard error	*t* value	*P* value		Edf	*F*	*P* value
Intercept	2.19	0.16	14.05	<0.001	Proportion of other zooplankton	2.92	15.20	<0.001
Preferred food	1.27	0.62	2.05	0.0489				
Model overview		R^2 adjusted: 0.56		AIC: 74.77				

Edf estimated degrees of freedom

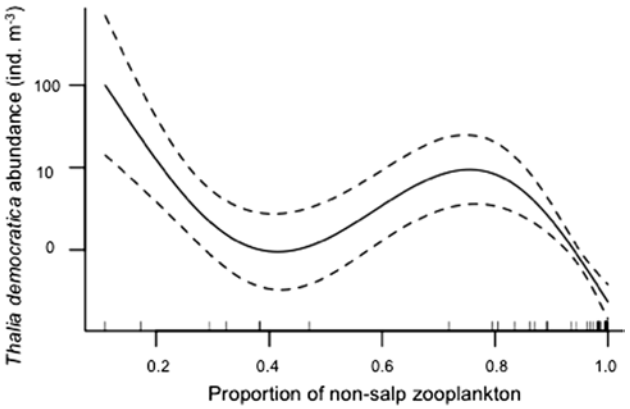

Fig. 8 Fitted smoother value for proportional non-salp zooplankton abundance as obtained through generalised additive mixed modelling analysis illustrating the nonlinear relationship with *T. democratica* abundance. *Tick marks* on the *x* axis are observed data points. The *y* axis represents fitted values. *Dotted lines* represent 95 % confidence intervals

environmental variables. We confirmed that the relationship between salp abundance and proportion of non-salp zooplankton was not due to spurious correlations using a randomised resampling approach (Brett 2004). Average *r* for the correlation between salp abundance and proportion of non-salp zooplankton when the variables were randomly resampled was 0.003 (SD = 0.17, 95 % confidence interval: −0.008 to 0.01). As the correlation coefficient of the original data ($r = -0.47$) exists outside of the distribution of the randomised data, we have indicated that the relationship was not spurious.

The GAMM originally included four explanatory variables: temperature, $\log_{10}$-chlorophyll *a*, proportion of non-salp zooplankton, and preferred food (>2 μm). Variables that were sequentially removed from the model were temperature followed by $\log_{10}$-chlorophyll *a.* The most parsimonious model included two significant terms: proportion of non-salp zooplankton and preferred food (Table 3). Log_{10}-transformed salp abundance was positively related to preferred food ($P < 0.05$, Table 3). As the relationship was nonlinear, a smoother plot was used to illustrate the effect of proportion of non-salp zooplankton on *T. democratica* abundance. Increasing proportion of non-salp zooplankton has a significantly negative relationship with $\log_{10}$-transformed salp abundance ($P < 0.001$, Fig. 8).

Discussion

Long-term *T. democratica* abundances in this study confirm the previous work that identifies spring as the most productive season for *T. democratica* (e.g. Tranter 1962; Licandro et al. 2006). This is most likely a result of high phytoplankton abundances after the spring bloom providing food for a developing salp swarm. There was significant variability in *T. democratica* abundances sampled during austral spring (September–November) voyages from 2008 to 2010. A tenfold difference in salp swarm size across three voyages indicates the highly variable nature of salp swarms, even during optimal conditions. Considering Heron and Benham's (1985) theory of overwintering (Fig. 1), we suggest that variations in swarm magnitude reflect changes in *T. democratica* condition. Measures of *T. democratica* condition, such as growth and asexual reproduction, would therefore also represent a measure of the nutrition received. This growth–fecundity trade-off is also seen in other organisms, such as nematodes and fruit flies, where dietary restriction results in reduced fecundity (Partridge et al. 2005). We show, however, that the opposite trend is seen in salps, where some form of dietary restriction (varied phytoplankton communities) results in increased asexual reproduction, most likely as a result of longer development time needed for reproductive effort (Lewontin 1965).

Long-term monitoring

The context and seasonality for our three voyages is provided by the long-term monthly observations at Port Hacking, showing swarm formation during the spring. Similar trends in *T. democratica* abundance were observed between the long-term monitoring at Port Hacking and in our three spring voyages. Direct comparisons between sampling months show that *T. democratica* abundances sampled at Port Hacking and during our voyages were of similar magnitude (Fig. 6a); however, statistical comparisons could not be undertaken due to only one haul being performed at

Port Hacking. *T. democratica* swarm abundance from the 2008 voyage was greater than the long-term October average obtained from Port Hacking. This was also the highest recorded abundance of *T. democratica* to date (Andersen 1998; Henschke et al. 2011). Higher than average abundances of *T. democratica* during spring blooms have previously been recorded near Port Hacking in 1940–1941 (Thompson and Kesteven 1942) and 1960 (Tranter 1962). Further sampling will be needed to indicate whether these high-magnitude swarms are a reoccurring trend. Despite large variability in *T. democratica* abundance across the long-term survey, similar relative abundances to our spring voyages suggest that salp swarms at the Port Hacking station may be broadly representative of conditions for the surrounding shelf. This is consistent with oceanographic modelling observations (Oke and Sakov 2012). Due to the patchy nature of salps, more extensive comparisons between the Port Hacking and other Australian National Reference Stations could be made using the recently commissioned Continuous Plankton Recorder program and with zooplankton sampled in surrounding shelf areas.

Experimental growth comparison

Experimental growth rates of *T. democratica* measured in this study (1.83–2.32 % length h^{-1}; Table 2) fall within the range of previously observed growth rates, from 0.3 % length h^{-1} (Deibel 1982) to 28 % length h^{-1} (Le Borgne and Moll 1986). It should be noted however that laboratory experiments (Heron 1972; Deibel 1982) resulted in the slowest growth rates of only 0.3–3 % length h^{-1}, whereas cohort tracking in the field and Heron and Benham's (1985) growth index resulted in the highest growth rates (Heron 1972; Le Borgne and Moll 1986; Tsuda and Nemoto 1992). Growth rates from 0.3 to 0.9 % length h^{-1} were obtained in laboratory experiments under low food concentrations (0.1–0.6 Chl-*a* μg L^{-1}) (Deibel 1982). Our growth rates were faster than those obtained by Deibel (1982), despite our experiments being performed at similar temperatures (20 °C). This variation was likely due to our experiments being performed at higher food concentrations (~1.1 Chl-*a* μg L^{-1}) that are more likely to happen during swarm formation. Similarly, Heron (1972) found growth rates of small individuals could vary from 1 % length h^{-1} when less food is available, to as high as 21 % length h^{-1} when food conditions are "optimal." Such fast growth rates in the laboratory, however, only occurred for embryos and "when extraordinary care was taken in collection and handling" (Heron 1972). The growth rates decreasing rapidly after birth to a maximum of 3 % length h^{-1} (Heron 1972), similar to our after birth growth rates (1.83–2.32 % length h^{-1}).

Timing of blastozooid chain release was between 0300 and 0800 hours and other studies agree with this observation (Miller and Cosson 1997; Heron and Benham 1984), suggesting that individuals used in our experiments were not adversely affected by capture. Predictable release times demonstrate that care must be taken when collecting samples for biomass and population demographic estimates during these spawning times, as swarm magnitude will be elevated as a result of mating aggregations at dawn (Heron 1972). Faster growth rates of *T. democratica* (>8 % length h^{-1}) were obtained from cohort tracking in the field (Heron 1972; Tsuda and Nemoto 1992). As sampling times were not mentioned in either study, to determine whether higher growth rates were a result of natural conditions or swarming aggregations, future cohort studies should take into account time-of-day effects. For the purpose of this study, zooplankton samples for abundance and biomass estimates during dawn and dusk were not incorporated in the results.

Measured growth rates in this study were less than the relative growth index by approximately an order of magnitude. Other studies that have applied Heron and Benham's (1985) growth index also calculated high growth rates similar to our range, from 25 to 28 % length h^{-1} (Le Borgne and Moll 1986). As the relative growth index is based on growth rates obtained through cohort tracking (Heron and Benham 1985), values are expected to be higher than growth rates obtained through laboratory experiments. Despite our growth rate experiments being performed on small individuals (~1.5 mm) who have been known to grow the fastest (Heron 1972), our experimental values were not comparable to the growth index. No laboratory study has been able to replicate the high growth rates observed by cohort tracking or Heron's (1972) "optimal" experimental techniques. The experimental results presented here offer a good indication of growth rate and suggest care must be taken when considering high growth rates obtained by cohort tracking or the relative growth index. Similar slopes for the growth index and our experimental growth rates with asexual reproduction, suggest that the relative change in growth rate identified by the growth index may be correct. Hence, we recommend that in future studies, the relative growth index should be presented as a unitless measurement.

Thalia democratica demography

Life history characteristics of the *T. democratica* swarms differed among the three voyages, in relation to declining swarm magnitudes. There was a significant increase in asexual reproduction (BPC) from 2008 to 2010 (Fig. 6b), and the proportion of blastozooids reaching maturity decreased. *T. democratica* swarms in 2008 had the highest abundance and fastest relative growth. Low asexual reproduction indicates that in 2008, conditions were more

suitable for the formation of large swarms, while declining abundance and relative growth in 2009 and 2010 indicates that extrinsic conditions were less suitable than in 2008. A similar trend was seen in Heron and Benham's (1985) samples across spring, summer, and winter where highest abundances and lowest asexual reproduction occurred in spring. Therefore, Heron and Benham's (1985) overwintering theory could also be an explanation for interannual variation in swarm magnitude.

Oceanographic influence on salp swarm magnitude

Temperature and salinity conditions in inner shelf water across the three sampling years all fell within tolerable ranges for *T. democratica* (11.5–25.6 °C; Thompson 1948). The largest environmental differences among years were evident in phytoplankton communities prior to and at the time of sampling. The influence of the EAC prior to sampling in the region in 2009 can be seen through the dominance of smaller prokaryotes in the phytoplankton that are typical of EAC water (Goericke and Repeta 1992) compared to the larger prymnesiophytes that dominated in 2008 (Fig. 5a). Despite being non-selective filter-feeders, *T. democratica* has different retention efficiency for different particle sizes, with greater than 80 % efficiency on large particles such as prymnesiophytes and diatoms, and only 40–50 % on particles <2 μm (Vargas and Madin 2004) such as the prokaryotes dominant in the EAC. Correspondingly, the generalised additive modelling revealed that *T. democratica* abundance was positively related to preferred food (>2 μm; Table 3). Although food abundance (as estimated by chlorophyll *a* concentration) was similar in 2008 and 2009, a dominance of smaller phytoplankton in 2009 (<2 μm) may have limited the ability of *T. democratica* populations to grow as fast or large as they did in 2008. Laboratory studies monitoring the effects of changing phytoplankton type on *T. democratica* growth and asexual reproduction are necessary to further elucidate this theory.

In 2010, phytoplankton communities were dominated by preferred food sizes (prymnesiophytes and diatoms); however, slower relative growth for the *T. democratica* swarm was observed. Corresponding to an observed tenfold increase in total zooplankton biomass excluding salps in 2010, additive modelling identified a negative relationship between *T. democratica* and non-salp zooplankton abundance (Fig. 8). A much lower percentage of *T. democratica* young reaching maturity in 2010 (Table 1) suggests that additional non-salp zooplankton abundance may have increased predation on younger individuals as well as competition for food. Smaller stages of *T. democratica* are generally more nutritious, similar to crustaceans (Heron et al. 1988), and have been shown to be prey items for carnivorous copepods and fish (Pakhomov et al. 2002).

Another scenario to consider is the timing of the *T. democratica* swarm development. In 2008, the *T. democratica* swarm may have begun forming soon after the phytoplankton bloom, resulting in an earlier dominance over the food abundance. A later development in 2010 may have resulted in a large pre-existing competitive and predatory zooplankton environment for the *T. democratica* swarm to develop in. Time series studies considering the time lag between phytoplankton blooms, zooplankton abundances, and *T. democratica* swarm development will help to identify how important the time of development is to the eventual swarm magnitude.

Concluding remarks

We have shown that salp life history characteristics such as asexual reproduction and growth rate were associated with interannual variations in abundance and thus may be major factors determining swarm magnitude. The negative relationship between asexual reproduction and abundance is consistent with Heron and Benham's (1985) overwintering theory. This relationship appears to be mainly influenced by nutritional availability, in particular phytoplankton type. Interannual variation in life history characteristics identified in this study confirms previous work that suggests *T. democratica* and other gelatinous species are effective indicators of changing oceanographic conditions (e.g. Thompson and Kesteven 1942; Hay 2006). Detailed laboratory studies could test our hypothesis that the prey field determines salp condition in order to determine causality for variation in salp swarm magnitudes. As *T. democratica* swarms are prevalent within other western boundary currents in the world (Deibel and Paffenhofer 2009), these results are globally relevant. The ability to predict patches and magnitude of salp swarms will be important for the management of the marine environment as a whole, but particularly for improving our understanding of the biogeochemical cycle due to the influential role of the mass depositions of carbon-rich faecal pellets and carcasses (Henschke et al. 2013) produced in salp swarms.

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