

Size-specific grazing and competitive interactions between large salps and protistan grazers

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Abstract

We investigated competition between *Salpa thompsoni* and protistan grazers during Lagrangian experiments near the Subtropical Front in the southwest Pacific sector of the Southern Ocean. Over a month, the salp community shifted from dominance by large (> 100 mm) oozoids and small (< 20 mm) blastozoids to large (~ 60 mm) blastozoids. Phytoplankton biomass was consistently dominated by nano- and microphytoplankton (> 2 μm cells). Using bead-calibrated flow-cytometry light scatter to estimate phytoplankton size, we quantified size-specific salp and protistan zooplankton grazing pressure. Salps were able to feed at a > 10,000 : 1 predator : prey size (linear-dimension) ratio. Small blastozoids efficiently retained cells > 1.4 μm (high end of picoplankton size, 0.6–2 μm cells) and also obtained substantial nutrition from smaller bacteria-sized cells. Larger salps could only feed efficiently on > 5.9 μm cells and were largely incapable of feeding on picoplankton. Due to the high biomass of nano- and microphytoplankton, however, all salps derived most of their (phytoplankton-based) nutrition from these larger autotrophs. Phagotrophic protists were the dominant competitors for these prey items and consumed approximately 50% of the biomass of all phytoplankton size classes each day. Using a Bayesian statistical framework, we developed an allometric-scaling equation for salp clearance rates as a function of salp and prey size:

$$\text{Clearance(ESD)} = \varphi \cdot \text{TL}^\psi \times \min\left(\frac{(\text{ESD}/\theta \times \text{TL}^\gamma)^2}{0.16 + (\text{ESD}/\theta \times \text{TL}^\gamma)}, 1\right) \times Q_{10}^{(T-12^\circ\text{C})/10}$$

where ESD is prey equivalent spherical diameter (μm), TL is *S. thompsoni* total length, $\varphi = 5.6 \times 10^{-3} - 3.6 \times 10^{-4}$, $\psi = 2.1 - 0.13$, $\theta = 0.58 - 0.08$, and $\gamma = 0.46 - 0.03$ and clearance rate is $\text{L d}^{-1} \text{ salp}^{-1}$. We discuss the biogeochemical and food-web implications of competitive interactions among salps, krill, and protozoans.

Salps play a unique ecological and biogeochemical role as large, gelatinous grazers that can feed rapidly and efficiently on some of the smallest phytoplankton in the ocean (Kremer and Madin 1992; Bone 1998; Sutherland et al. 2010). Indeed, salps can feed at one of the highest predator : prey size ratios (> 10,000 : 1) of any organism in the ocean (Kremer and

Madin 1992; Fuchs and Franks 2010). Their rapidly beating muscle bands also allow them to routinely filter > 1000 times their biovolume per hour (Harbison and Gilmer 1976; Madin et al. 2006). By compacting microscopic prey into very large, rapidly sinking fecal pellets, their blooms can reshape pelagic biogeochemical pathways and increase CO₂ sequestration in the deep ocean (Bruland and Silver 1981; Madin 1982). However, as a result of their patchy distributions, poor preservation during typical net tows, and difficulties associated with experimental work with gelatinous taxa, they remain understudied (Henschke et al. 2016).

Traditionally, and especially in the Southern Ocean, salps have been considered competitors of crustaceans, especially the Antarctic krill, *Euphausia superba* (Loeb et al. 1997; Pakhomov et al. 2002). The assumption of competitive interactions

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between these groups is driven, in part, by their roughly similar sizes and collection by the same methodology (net tows). However, *E. superba* feed preferentially on large diatoms (Haberman et al. 2003), while salps are largely nonselective feeders that can efficiently consume all nano- and microphytoplankton, and less efficiently consume picophytoplankton (Kremer and Madin 1992; Sutherland et al. 2010). Salps also have distinctly different life cycles than crustaceans. Their alternation of generations, featuring solitary asexual oozoid phases and chain-forming sexual blastozooids, allows rapid population growth on time scales of days to weeks in warm temperatures and weeks to months in the Southern Ocean (Bone 1998; Luskow et al. 2020). In contrast, *E. superba* has a multi-year life cycle, with population fluctuations linked to interannual climate variability (Pakhomov 2000; Saba et al. 2014).

Given these considerations, we ask whether phagotrophic protists may potentially be more important competitors of salps. Phagotrophic protists (heterotrophs and mixotrophs) are taxonomically diverse and the dominant grazers of picoplankton (Sherr and Sherr 1994; Caron et al. 2012). They also consume from 59% to 75% of all phytoplankton production across diverse marine ecosystems, including in some of the coldest waters near the Antarctic continent (Calbet and Landry 2004; Garzio et al. 2013). These grazers have rapid growth rates, potentially higher than a doubling per day at tropical temperatures, and higher than a doubling per week even at the coldest temperatures in the Southern Ocean (Hansen et al. 1997). Considering these similarities in prey and growth rates, phagotrophic protists are likely more important as competitors of salps than crustaceans, although the consumers of salps and protists are likely very different. Bacterivorous and herbivorous protists are themselves important prey for other phagotrophic protists and play a significant role in supporting metazoan zooplankton in many ecosystems (Calbet 2008; Landry et al. 2020). With sizes (linear dimension) two to four orders of magnitude greater than protists, however, salps are primarily consumed by either nekton or specialized crustacean micro-predators, including hyperiid amphipods (Madin and Harbison 1977; Henschke et al. 2016).

To test the hypothesis that salps and protistan grazers compete for prey, we conducted a series of protistan and salp grazing experiments during Lagrangian studies conducted near the Chatham Rise in water parcels with blooms of *Salpa thompsoni*. The Chatham Rise is a topographic feature that extends 1000 km east of New Zealand. This region is characterized by strong latitudinal gradients with the Subtropical Front (STF) separating warmer, N-limited subtropical waters to the north from colder, Fe-limited subantarctic waters. The collocation of the STF with this topographic feature leads to increased mixing and productivity (Sutton 2001; Chiswell et al. 2013). Most of this primary productivity is consumed by protistan zooplankton, and these protists in turn serve as important components of crustacean diets (Zeldis and Décima 2020). Previous studies have also shown the common presence of salp swarms in the

region (Bradford 1985; Zeldis et al. 1995), allowing us to conduct experiments to target salp and protist interactions. We assessed the in situ size spectra of phytoplankton and quantified size-specific grazing rates of both protists and *S. thompsoni*. Our results show that *S. thompsoni* efficiently consumes most nano- and microphytoplankton, and their small blastozooids also feed on picophytoplankton. However, *S. thompsoni* blastozooids and oozoids derived the majority of their nutrition from nano- and microphytoplankton. Phagotrophic protists were the dominant predators on all size classes of phytoplankton, highlighting their importance as competitors of salps, although salps can also efficiently consume these phagotrophic protists.

Methods

Cruise design

We used a Lagrangian process study design to conduct detailed investigations of salp and protist grazing pressure near the Chatham Rise in November 2018 during the Salp Particle expOrt and Oceanic Production (SalpPOOP) expedition on board the RV *Tangaroa*. We used information from historical zooplankton sampling in the region and the distributions of fish taxa that prey on salps to identify regions with high likelihood of salp presence. We then conducted an aerial survey with approximately hourly net tows to identify water parcels with high salp abundance and used Lagrangian drift arrays to track these water parcels while conducting detailed investigation of the evolving plankton community over periods ranging from 4 to 8 d (hereafter referred to as Lagrangian “cycles”). One Lagrangian drift array (which we refer to as the “incubation array”) consisted of a satellite-enabled surface float, a 3 × 1 m holey-sock drogue centered at 15-m depth in the mixed layer, and metal loops at 18 depths allowing us to affix mesh bags containing experimental bottles to be incubated in situ (Landry et al. 2009). We conducted three Lagrangian experiments (hereafter referred to as “cycles”) in waters with salps and focus on these results here, although two additional cycles were conducted in nonsalp waters (Fig. 1).

During each cycle, we collected samples for phytoplankton analyses from daily CTD casts at ~ 02:00 local time. Samples included flow cytometry and size-fractionated chlorophyll *a* (Chl *a*) (< 2 μm, 2–20 μm, >20 μm) at six depths. We sampled from the same depths and casts for daily 24-h incubations, using the two-point dilution technique (Landry et al. 1984) coupled to flow-cytometry analysis to quantify size-specific protistan grazing rates in situ. We also conducted twice daily oblique bongo net tows (0.71 m diameter, 200 μm mesh) from the surface to 200 m depth at approximately local noon and midnight to quantify salp abundance, size structure, and gut pigment content. A second type of net, which we refer to as a “salp net” (1-m diameter, 200 μm mesh, with a large [30-L] nonfiltering polycarbonate cod end), was used to

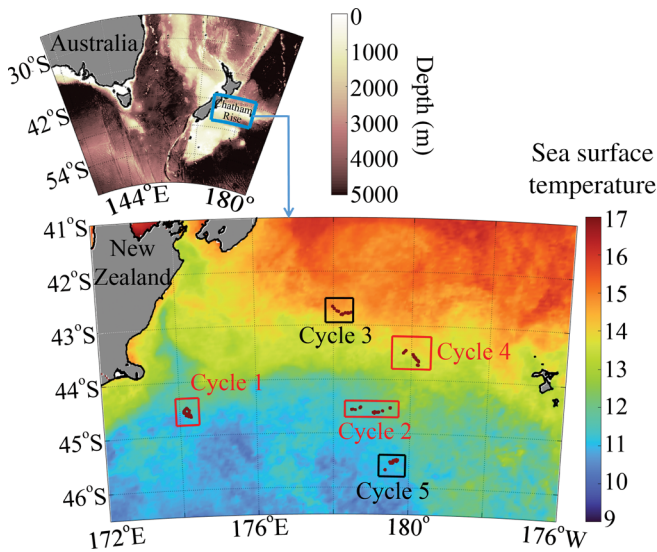


Fig. 1. Study region. Upper plot shows bathymetry of the broader oceanographic region. Lower plot shows our study area with monthly average SST (NASA MODIS satellite). Net tow locations are indicated with red dots. Red rectangles indicate locations of +Salp Lagrangian cycles. Black squares represent locations of cycles with few or no salps.

collect salp specimens for experimental work, including incubations to quantify salp grazing pressure. For detailed information, see Online Supplementary Methods 1.

Salp abundance and biomass estimation

Zooplankton net tows were conducted at least twice daily (day and night) to a depth of 200 m. Salps were sorted, measured for length, identified to species, and staged into oozyoid (solitary) or blastozoid (aggregate). A subsample from each tow was taken for determination of Chl *a* in salp guts. *S. thompsoni* total lengths were divided into 5 mm bins (5–140 mm) from which we computed normalized abundance size spectra (NASS = salp abundance within a bin divided by bin width).

Protistan grazing experiments

We conducted daily two-point in situ protistan grazing dilution experiments at six depths in the water column (Landry et al. 1984, 2009). A control bottle and a “dilute” treatment bottle (25% whole seawater : 75% 0.1- μ m filtered seawater) were incubated in situ on the drifting array for 24 h. Initial and final samples were taken for flow cytometry and Chl *a* analyses. Daily specific mortality rates due to protistan grazing were calculated as: $m = (k_{\text{dil}} - k_{\text{whole}}) / (1 - \text{dil})$, where k_{dil} is the growth rate in the diluted treatment bottle, k_{whole} is the growth rate in the control bottle, and dil is the fraction of whole seawater in the dilute treatment bottle (25%).

Salp grazing experiments

To determine the size-specificity of salp grazing, we conducted grazing incubations in 20-liter plankton kreisels or

30-liter pseudo-kreisels filled with mixed layer seawater. Salps were collected via short, slow tows through the mixed layer with the salp net. Healthy specimens were transferred into one of the paired kreisels, while the second kreisel was used as a control treatment. We incubated *S. thompsoni* blastozoids and oozyoids ranging in size from 50 to 128 mm total length. We also conducted three incubations with a chain of blastozoids (6–8 mm individuals) released by an oozyoid inside of one of the plankton kreisels. We found that this was the only way to successfully obtain such small blastozoids in healthy conditions. Incubations typically lasted ~ 24 h and were sampled every ~ 2 h for flow cytometry.

Gut pigment measurements

Because previous studies have shown that salp filtration rates can be underestimated when salps are incubated in a tank (Pakhomov et al. 2002), we also collected organisms for gut pigment analysis from bongo tows conducted multiple times daily (Madin and Cetta 1984). Chl *a* and phaeopigment content (together GPig, units = μg Chl *a* equivalents salp^{-1}) in excised guts was measured using the acidification method (Strickland and Parsons 1972; Décima et al. 2019). We estimated gut pigment turnover (GPT) time using the following equation $\text{GPT (h)} = 2.607 \times \ln(\text{OAL, mm}) - 2.6$. Chlorophyll-based grazing was estimated as: $G (\mu\text{g Chl } a \text{ equiv. salp}^{-1} \text{ h}^{-1}) = \text{GPig} \times \text{GPT}^{-1}$.

Flow cytometry

Flow cytometry samples from the water column, protistan grazing dilution experiments, and salp incubations were analyzed at sea to estimate the abundance and size of eukaryotic phytoplankton. Cell diameter was estimated from forward light scatter calibrated with polystyrene beads. Biomass was estimated from diameter using equations in Menden-Deuer and Lessard (2000).

Size-specific grazing rate calculations

From flow cytometry samples in salp and protistan grazing rate experiments, we calculated normalized biomass size spectra (NBSS) for eukaryotic phytoplankton from 0.8 to 31 μm . We calculated the normalized biomass as:

$$B_n(\text{ESD}) = \sum_{\frac{\text{ESD}}{2}}^{2 \times \text{ESD}} \text{Biomass} / (2 \times \text{ESD} - \text{ESD} / 2) \quad (1)$$

Phytoplankton mortality due to protistan grazing as a function of size was computed from initial and final NBSS for each experiment. To determine an average grazing rate for each Lagrangian cycle, we averaged all grazing rate estimates, $m(\text{ESD})$, made in the mixed layer during that cycle. We used results from these in situ protistan grazing experiments to compute protistan grazing rate-corrected size-specific mortality of

phytoplankton due to salp grazing in our on-deck incubations (G , units of d^{-1}) as:

$$G(\text{ESD}) = \frac{m(\text{ESD}) \left(\left(\frac{\text{vol}}{f_i N} \right) \left(e^{-\frac{f_i \times N}{\text{vol}} t} - 1 \right) + t \right) - \ln \left(\frac{B_{n,t}(\text{ESD}, t)}{B_{n,c}(\text{ESD}, t)} \right)}{t} \quad (2)$$

where $B_{n,c}$ is the normalized biomass in the control kreisel at time t , $B_{n,t}$ is the normalized biomass in the treatment kreisel (with salps) at time t , vol is the volume of the kreisel, N is the number of salps in the treatment kreisel, and f_i is an initial estimate of salp filtration rate. Throughout this manuscript, we use the term “filtration rate” to refer to the volume of water pumped through a salp per unit time (which is independent of prey cell size), while we use the term “clearance rate” to refer to the volume of water cleared by salps of a particular prey size per unit time. Clearance rate is thus less than or equal to filtration rate and varies for differently sized prey. $G(\text{ESD})$ relates to the actual clearance rate of the salps (C , units of $\text{L salp}^{-1} \text{d}^{-1}$) through the equation: $C(\text{ESD}) = G(\text{ESD})/N/\text{vol}$. For derivation of Eq. 2, see Supp. Methods 3. For additional details on all field methods, see Supp. Methods 1.

Bayesian parameter estimation and model selection

For every salp incubation, we calculated clearance rate as a function of prey ESD using two simple models. The first assumes clearance rates depend only on the filtration rate and filter mesh of the salp and uses a two-parameter function in which F is the filtration rate of the salp and τ is a parameter that is approximately equal to the equivalent mesh size of the salp:

$$\text{Clearance}(\text{ESD}) = \min \left(\frac{(\text{ESD}/\tau)^2}{0.16 + (\text{ESD}/\tau)^2}, 1 \right) \times F \quad (3)$$

The second equation is a three-parameter model that adds a functional form representing potential escape responses of prey, assuming that prey swimming velocity is proportional to size:

$$\text{Clearance}(\text{ESD}) = \min \left(\frac{(\text{ESD}/\tau)^2}{0.16 + (\text{ESD}/\tau)^2}, 1 \right) \times e^{-\lambda \text{ESD}} \times F \quad (4)$$

where λ is a parameter that describes the evasion success of prey. Derivation of these equations is given in Supp. Methods 4. To fit these parameters to the incubation data, we used a Bayesian statistical framework (see Supp. Methods 2). To objectively choose whether Eq. 3 or 4 was more appropriate for each incubation, we used deviance information criterion (DIC; Spiegelhalter et al. 2002).

To quantify the salp-size-dependence of filtration rate and equivalent mesh size, we also fit allometric-scaling relationships to the data from all incubations:

$$\text{Clearance}(\text{ESD}) = \varphi \times \text{TL}^\psi \times \min \left(\frac{(\text{ESD}/\theta \times \text{TL}^\gamma)^2}{0.16 + (\text{ESD}/\theta \times \text{TL}^\gamma)^2}, 1 \right) \times Q_{10}^{(T-12^\circ\text{C})/10} \quad (5)$$

$$\text{Clearance}(\text{ESD}) = \varphi \times \text{TL}^\psi \times \min \left(\frac{(\text{ESD}/\tau)^2}{0.16 + (\text{ESD}/\tau)^2}, 1 \right) \times Q_{10}^{(T-12^\circ\text{C})/10} \quad (6)$$

where TL is salp total length, $\varphi \times \text{TL}^\psi$ is an allometric-scaling relationship for the filtration rate, $\theta \times \text{TL}^\gamma$ is an allometric-scaling relationship for τ (equivalent mesh diameter), T is temperature, and Q_{10} is a temperature scaling factor that we assume is equal to 2 (Madin and Purcell 1992). Equation 6 assumes that τ does not vary with salp size. We again chose between the two equations based on DIC.

Because salp filtration rates are often lower in incubations than in situ (Pakhomov et al. 2002), we also fit Eq. 5 (which was found to be a better predictor than Eq. 6) to gut pigment data results. For this analysis, we combined in situ mixed layer carbon-based NBSS with mixed layer size-fractionated Chl a measurements to determine in situ Chl a -based NBSS. We then fit Eq. 5 to the results of Chl a -based consumption rates ($\text{mg Chl } a \text{ h}^{-1}$) determined from gut pigment measurements.

Results

Environmental conditions and salp abundances

We found salps in three water parcels in the vicinity of the Chatham Rise and the STF (Fig. 1). The highest salp abundance was found in a *S. thompsoni*-dominated coastal region in modified subantarctic water (Cycle 1). Surface Chl a was $0.9 \mu\text{g L}^{-1}$ and surface temperature was 11°C . Cycle 2, conducted further offshore and in subantarctic water along the southern flank of the STF, featured a mixed salp community, with substantial abundances of *S. thompsoni*, but also other abundant taxa including *Pegea confederata* and *Thetys vagina* (although we only present results from *S. thompsoni* in this manuscript). Surface Chl a was substantially lower ($0.4 \mu\text{g L}^{-1}$) and surface temperature was 10°C . During Cycle 4, we sampled a region of mixed water featuring characteristics representative of subtropical water that had likely experienced mixing with subantarctic water near the STF. Surface temperature on Cycle 4 was $\sim 13^\circ\text{C}$ and surface Chl a was $1.3 \mu\text{g L}^{-1}$. Heterotrophic bacteria abundance in the surface mixed layer averaged 9.3×10^5 , 1.4×10^6 , and 2.6×10^6 cells mL^{-1} , in Cycles 1, 2, and 4, respectively. Euphotic zone depths (to 1% of surface irradiance) were relatively shallow at 32, 35, and 25 m for Cycles 1, 2, and 4, respectively, and surface mixed layer depths were 23, 48, and 21 m, respectively. We also conducted two cycles in subtropical (Cycle 3) and subantarctic (Cycle 5) waters without salp blooms. Hydrographic properties and phytoplankton abundance during these cycles were largely similar to those encountered during Cycles 4 and 2, respectively.

The size structure of the *S. thompsoni* population varied substantially between cycles (Fig. 2). Cycle 1 was the only cycle with a high abundance of large oozoids (80–130 mm), and

small (~ 10 and ~ 40 mm) blastozoids were also abundant. Cycle 2, which appeared to represent a temporal progression of the bloom encountered in Cycle 1, was dominated by medium-sized blastozoids (25–50 mm), with very few oozoids present. By Cycle 4 (approximately 1 week later), the salp community was dominated by large blastozoids (50–70 mm) and a new generation of small oozoids appeared.

Phytoplankton size spectra and protistan grazing

The phytoplankton normalized biomass size spectrum varied between cycles, although phytoplankton biomass consistently peaked near the upper end of the nanophytoplankton size range (i.e., 7–20 μm ; Fig. 3). During Cycle 1, the cycle with the highest salp abundance and also the closest to land, there was a substantial abundance of picoeukaryotic phytoplankton (0.5–1 μm), comparatively few phytoplankton with an ESD of ~ 2 μm , and a greater biomass of 5–30 μm phytoplankton than smaller taxa. During Cycles 2 (salps) and 5 (no salps), which were both conducted in water of primarily subantarctic origin, there were fewer picoeukaryotic phytoplankton and carbon biomass increased nearly monotonically with size from picophytoplankton to a peak at ~ 15 μm ESD. Cycles 3 (no salps) and 4 (salps) in subtropical water featured fairly consistently low biomass of phytoplankton from 0.5 to 3.0 μm , followed by a rapid increase in biomass with increasing size to a peak at ~ 8 μm .

Across cycles and size classes, protists consumed $\sim 50\%$ of phytoplankton biomass per day (Fig. 4), with some variability

between cycles. For instance, phytoplankton mortality due to protistan grazing was higher for microplankton than for pico- and nanoplankton during Cycle 2, but fairly similar to or slightly lower than mortality of nanoplankton for Cycles 1 and 4. These differences, however, were not statistically significant, and we found no significant difference between protistan grazing rates during nonsalp cycles (Fig. 4a) and salp cycles (Fig. 4b). However, we note that uncertainty was substantial for microplankton, because these cells were far less abundant than pico- and nanophytoplankton so their abundance estimates based on small volumes analyzed by flow cytometry are inherently more variable.

Salp grazing incubations

We used a Bayesian statistical framework to combine flow cytometry-derived phytoplankton abundance changes in salp incubations into size-specific estimates of salp clearance rates (Fig. 5). Small blastozoids (Fig. 5a) had maximum clearance rates < 0.1 $\text{L salp}^{-1} \text{d}^{-1}$. The youngest salps had substantially lower grazing rates than even 3-d old (8 mm) blastozoids. The 8-mm blastozoids fed efficiently even on phytoplankton < 1 μm in diameter. Larger blastozoids (Fig. 5b) and oozoids (Fig. 5c) had filtration rates that ranged from 2 to 30 $\text{L salp}^{-1} \text{d}^{-1}$, with no clear dependence on their size (Fig. 5d).

The equivalent mesh size (r), which is essentially the prey size below which clearance rate begins to decrease substantially, was typically 2–3 μm (Fig. 5e). However, it was substantially lower for 8-mm blastozoids (0.4 μm). Contrarily, the smallest blastozoids (6 mm) had the largest equivalent mesh size (6 μm), although this newly released chain appeared to be only weakly feeding. Only 4 of 10 incubations showed statistically significant evidence for prey avoidance at large prey sizes, and these experiments contained organisms that were feeding with lower filtration rates than other similarly sized salps. Since previously published evidence suggests that salp filtration rates are higher in situ than in tank experiments, this leads us to believe that prey avoidance behaviors did not significantly reduce filtration rates on the size of prey we assessed (0.7–30 μm). This does not, however, suggest that larger prey taxa with stronger swimming behaviors (e.g., crustacean nauplii) cannot successfully avoid capture by salps.

To further investigate allometric grazing relationships, we constrained Eqs. 5 and 6 using all incubation data. The DIC computed after fitting Eq. 5 (which includes allometric scaling of the equivalent mesh size) was lower than for Eq. 6 (3.51×10^4 vs. 3.65×10^4) suggesting that it is a better fit to the data. Parameters fit with this model were: $\varphi = 1.5 \times 10^{-3} \pm 1.4 \times 10^{-4}$, $\psi = 2.1 \pm 0.02$, $\theta = 0.55 \pm 0.08$, and $\gamma = 0.45 \pm 0.03$. For perspective, these results suggest that the equivalent mesh size of a salp increases from 1.2 μm for a 6-mm salp to 4.7 μm for a 125-mm salp, while the filtration rate increases from 0.06 to 39.9 $\text{L salp}^{-1} \text{d}^{-1}$.

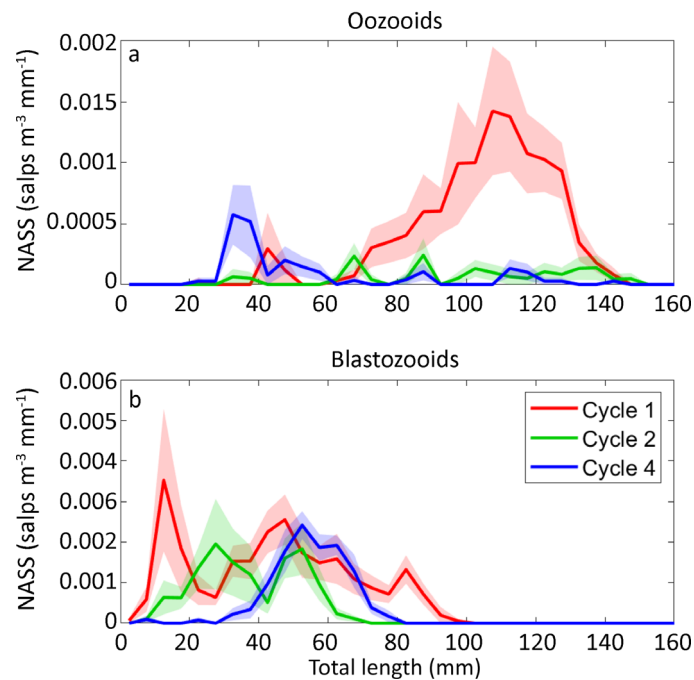


Fig. 2. Normalized abundance size spectra (NASS, $\text{salps m}^{-3} \text{mm}^{-1}$) as a function of the length of *Salpa thompsoni* oozoids (a) and blastozoids (b) in each cycle.

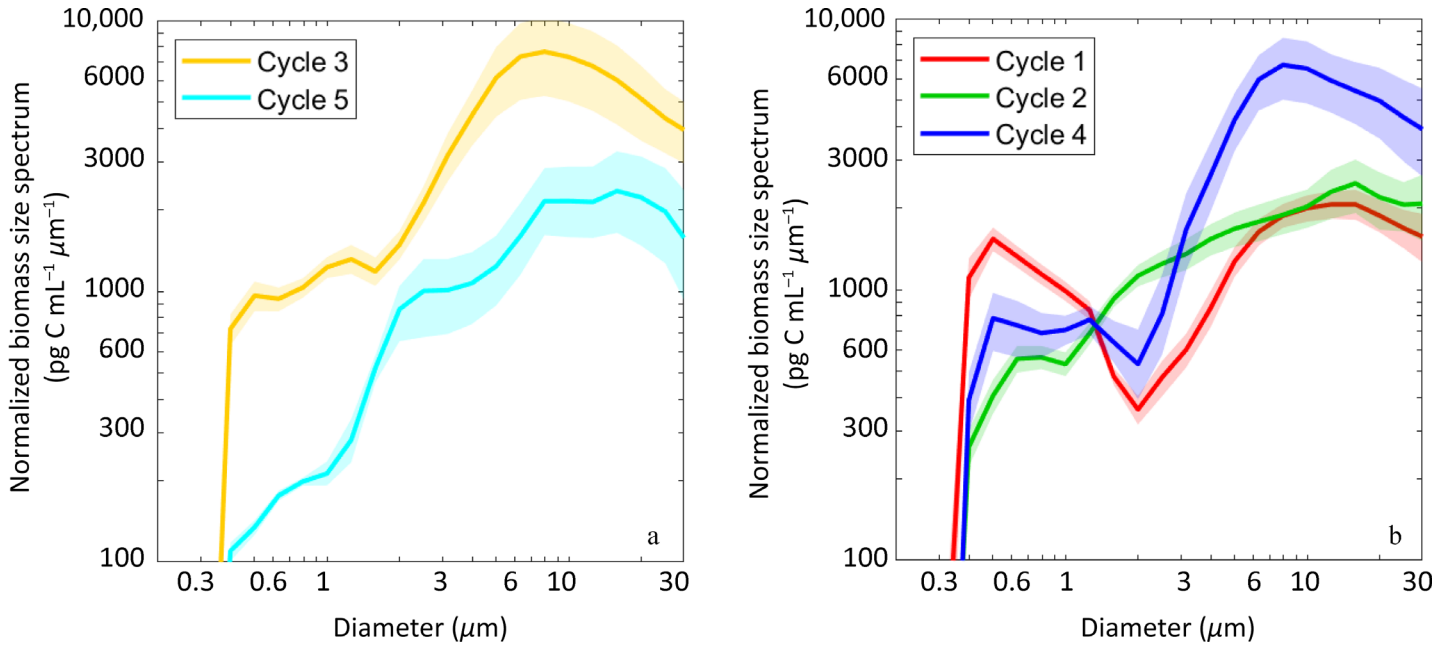


Fig. 3. Normalized biomass size spectra (pg C mL⁻¹ μm⁻¹) as a function of prey diameter (μm) of mixed layer eukaryotic phytoplankton communities for nonsalp cycles (a) and salp cycles (b). Shaded areas are 95% confidence intervals.

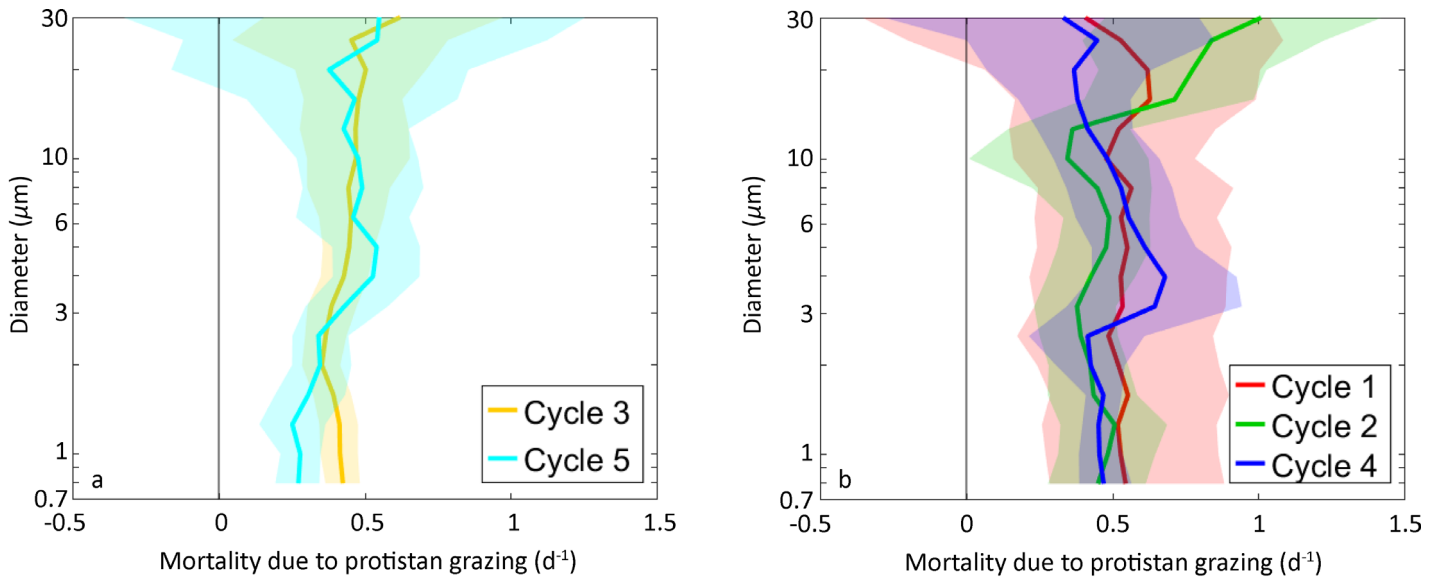


Fig. 4. Phytoplankton mortality due to protistan grazing (d⁻¹) as a function of prey diameter (μm) for nonsalp cycles (a) and salp cycles (b). Results are from multiple repeated grazing experiments conducted in situ at multiple depths spanning the mixed layer. Cycle averages are shown in heavier lines, whereas 95% confidence limits are shaded.

Salp grazing rates in situ

We measured the gut pigment content of 776 salps ranging in length from 6 to 150 mm. This included 521 blastozooids ranging from 9 to 97 mm and 255 oozoids ranging from 21 to 150 mm. These estimates were used to quantify in situ salp grazing rates (μg Chl *a* salp⁻¹ d⁻¹), which were combined with size-fractionated Chl *a* measurements from the mixed

layer to constrain Eq. 6 using in situ data (Fig. 6). Parameters fit with this model were: $\varphi = 5.6 \times 10^{-3} \pm 3.6 \times 10^{-4}$, $\psi = 2.1 \pm 0.13$, $\theta = 0.58 \pm 0.08$, and $\gamma = 0.46 \pm 0.03$. Notably, the value for ψ (exponent of the filtration rate to salp length relationship) was very close to the equivalent parameter determined from incubation results. However, φ (the intercept) was nearly a factor of 4 greater, suggesting that salp filtration rates

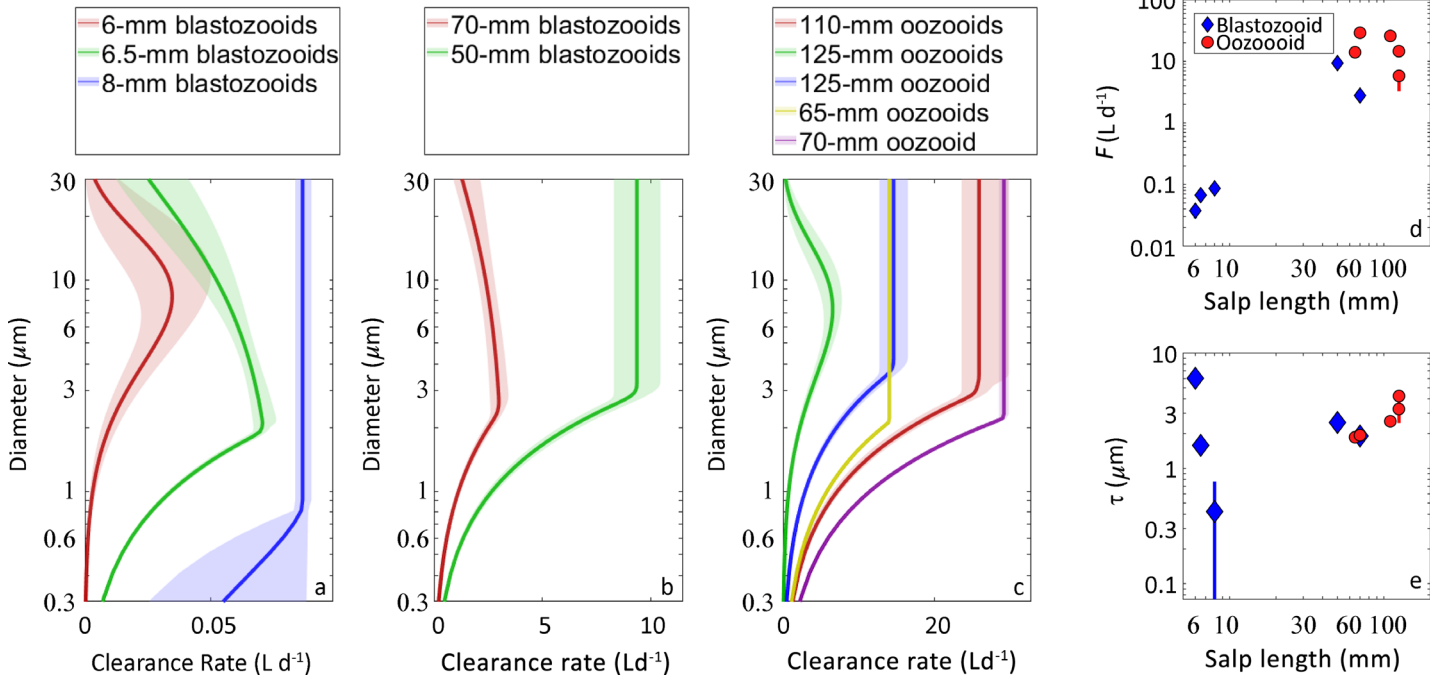


Fig. 5. Salp clearance rates ($L \text{ salp}^{-1} \text{ d}^{-1}$) as a function of prey diameter (μm) estimated from deckboard *Salpa thompsoni* grazing experiments conducted in plankton kreisels: small blastozooids (a), large blastozooids (b), large oozoids (c). Colors indicate different salp incubation experiments. Salp filtration rate (F , $L \text{ d}^{-1}$) as a function of total salp length (mm) (d). Effective filter mesh size (τ , μm) as a function of total salp length (mm) (e).

were approximately four times greater in situ than in the plankton kreisels. Using the results of our analysis, we estimate that a 6-mm, newly released blastozooid filtered $0.24 L \text{ salp}^{-1} \text{ d}^{-1}$, while a 150-mm oozoid filtered $208 L \text{ salp}^{-1} \text{ d}^{-1}$. We also estimate that the equivalent mesh spacing (τ) ranged from 1.3 to $5.8 \mu\text{m}$.

Equation 6 and the in situ parameterization allow us to quantify volume-specific salp clearance rates for different prey sizes. As expected, because $\psi < 3$, specific clearance rates decrease with increasing size. The smallest salps assessed in our study ($\sim 6 \text{ mm}$) had clearance rates of $\sim 12,000$ body volumes per day for prey $> 1.6 \mu\text{m}$. These small salps were fairly efficient at feeding on even smaller prey. For instance, their filtration rate on $0.8 \mu\text{m}$ cells was ~ 6000 body volumes per day. Volume-specific filtration rates were substantially lower for the largest salps collected in our study (150 mm). These salps had clearance rates of ~ 4000 body volumes d^{-1} for cells $> 6 \mu\text{m}$, but < 300 body volumes d^{-1} for $0.8 \mu\text{m}$ cells. We caution that these results may potentially underestimate salp clearance rates, because they assume that the salps were actively feeding at the time of collection and that all salps were feeding in the mixed layer, although our net tows went to a depth of 200 m. It is possible that the salps in Fig. 6 with low apparent grazing rates (relative to their size) were actually living beneath the euphotic zone, thus even high clearance rates would yield low gut pigment content.

We then used in situ salp abundances (Fig. 2) to quantify the clearance rates of the entire salp community. Although

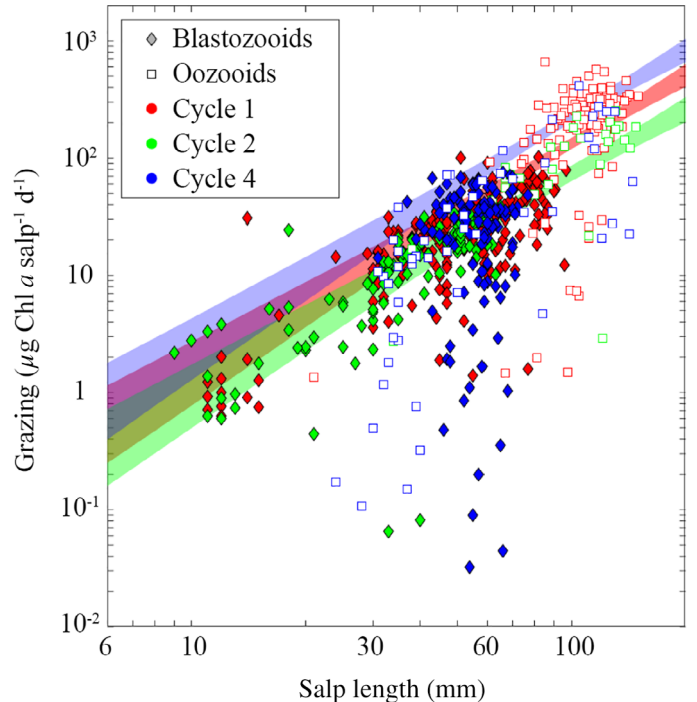


Fig. 6. Salp grazing rates ($\mu\text{g Chl } a \text{ salp}^{-1} \text{ d}^{-1}$) as a function of salp length (mm) determined from in situ gut pigment measurements for all cycles and for blastozooids and oozoids. Colored lines show Bayesian estimates of grazing as a function of *Salpa thompsoni* length (accounting for in situ mixed layer temperature and normalized Chl *a* size spectra for each cycle).

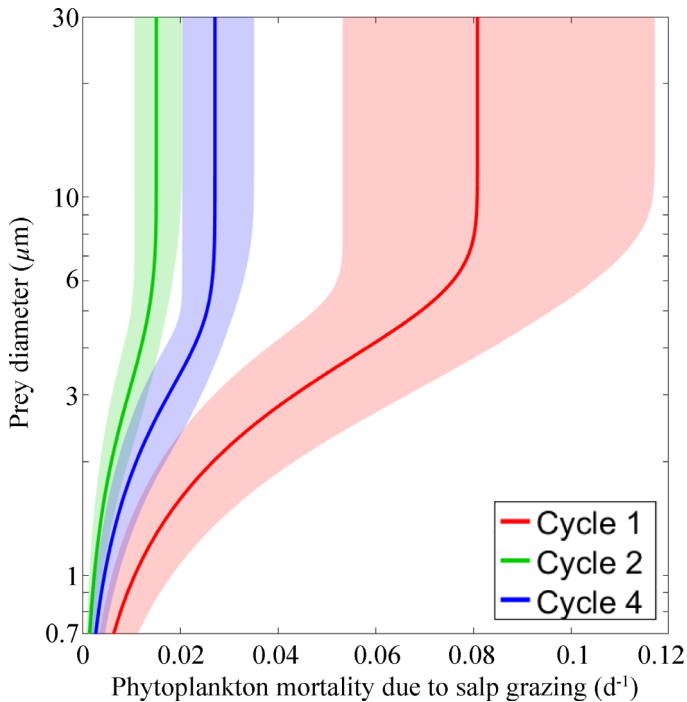


Fig. 7. Phytoplankton mortality (d^{-1}) due to grazing of the *Salpa thompsoni* community as a function of prey diameter (μm) for each cycle. Results are derived from Eq. 6 with in situ parameterization and cycle-specific salp abundance.

net tows were made to a depth of 200 m, we assumed in this calculation that all salps were collected in the euphotic zone. While this may overestimate salp abundance in the euphotic zone, it is offset by our previous assumption that all salps were collected in the mixed layer leading to an underestimate of clearance rates. For Cycle 1, with the highest salp abundance, salp grazing pressure cleared 8.1% of the biomass of $> 6\text{-}\mu\text{m}$ phytoplankton each day (Fig. 7). Smaller phytoplankton had lower mortality rates due to salp grazing (4.3% and 1.1% d^{-1} for 3- and $1\text{-}\mu\text{m}$ phytoplankton, respectively). Salp grazing pressure was lower during the other cycles (1.5% d^{-1} for large cells in Cycle 2; 2.7% d^{-1} in Cycle 4).

Because most phytoplankton carbon was contained in $> 5\text{-}\mu\text{m}$ nano- and microphytoplankton that were efficiently preyed upon by all salp sizes, the median (carbon-weighted) prey size was relatively invariant with salp size. Median prey size was similar at $8\text{--}9\ \mu\text{m}$ for salps in all cycles. This shows a $\sim 1000 : 1$ average predator : prey size ratio (linear dimension) for the smallest blastozooids collected in our study and a $> 10,000 : 1$ average predator : prey ratio for large oozooids.

Total ingestion was determined primarily by nano- and microphytoplankton prey concentration (which varied between the three cycles) and filtration rate. During Cycles 1 and 2, the smallest salps consumed $4\text{--}5\ \mu\text{g C}$ from phytoplankton daily, while during Cycle 4 they consumed $> 10\ \mu\text{g C d}^{-1}$. Larger organisms consumed substantially more, with

60-mm salps (large blastozooids) consuming $90\text{--}120\ \mu\text{g C d}^{-1}$ during Cycles 1 and 2 and nearly $300\ \mu\text{g C d}^{-1}$ during Cycle 4. 150-mm salps (large oozooids) consumed $300\text{--}400\ \mu\text{g C d}^{-1}$ during Cycles 1 and 2 and nearly $1000\ \mu\text{g C d}^{-1}$ during Cycle 4. These estimates are likely underestimates of total ingestion, since they include only eukaryotic phytoplankton biomass. Aplastidic protists, cyanobacteria, and heterotrophic bacteria were also abundant and likely to be important prey items of *S. thompsoni*.

Discussion

Salp grazing rates, daily ration, and size selectivity

Our results show strong size dependence of clearance rates for *S. thompsoni* spanning a range of sizes and including both oozooids and blastozooids. Absolute clearance rates for the largest oozooids were > 2 orders of magnitude higher than clearance rates for the smallest, newly released blastozooids (Fig. 5). However, since the exponent of the power-law relationship relating salp total length to filtration rate (2.1 ± 0.02) was lower than the exponent relating salp volume to length (2.45; Iguchi and Ikeda 2004), salp volume-specific clearance rates were inversely related to length, decreasing from $\sim 12,000\ \text{d}^{-1}$ for newly released blastozooids to $\sim 4500\ \text{d}^{-1}$ for large oozooids. Similarly, Madin et al. (2006) and Pakhomov et al. (2006) found that clearance rate normalized to organism biovolume decreased slightly with increasing size for *Salpa aspera* and *S. thompsoni*, respectively.

Combining Eq. 5 with phytoplankton size spectra data, we found that carbon-based ingestion rates increased from 4 to $12\ \mu\text{g C d}^{-1}$ for a typical newly released ($6\ \text{mm}$) blastozooid to $300\text{--}1000\ \mu\text{g C d}^{-1}$ for a 150-mm oozooid. Using results from Iguchi and Ikeda (2004) to estimate carbon mass from total length, we estimate that a 6-mm blastozooid had a carbon mass of $31\ \mu\text{g C}$, suggesting that these salps were consuming an equivalent of between 13% and 39% of their carbon mass each day. For comparison, using both cohort-based growth analysis across wide size ranges and in situ experiments within a plankton kreisel, Luskow et al. (2020) estimated length-based growth rates for *S. thompsoni* at the Chatham Rise of $\sim 10\% \text{ d}^{-1}$, which equates to a carbon-based growth rate of $\sim 26\% \text{ d}^{-1}$. Based on these calculations, a typical newly released blastozooid would consume barely enough phytoplankton carbon to meet its growth needs (neglecting carbon lost to respiration or defecation). However, *S. thompsoni* is likely to consume many other prey items. Heterotrophic bacteria biomass ranged from 5.9 to $37\ \mu\text{g C L}^{-1}$ in the mixed layer. Heterotrophic protists often have a biomass in the range of half of the phytoplankton biomass in the open ocean. *S. thompsoni* has also been shown to feed on a diverse suite of organisms larger than the $30\text{-}\mu\text{m}$ size cutoff that we used for phytoplankton, including eggs, nauplii and adult crustaceans, foraminifera, radiolarians, phaeodarians, pteropods, and nonliving detritus

including fecal pellets (Gowing 1989; Lancraft et al. 1991; von Harbou et al. 2011). Given these additional likely prey types, our grazing results seem remarkably consistent with simultaneous, but independent, measurements of growth rates.

Other studies have found variable ingestion rates for *S. thompsoni*. von Harbou et al. (2011) found that daily ingestion could exceed body weight in the summer in the Lazarev Sea (although at substantially higher surface Chl *a* than at our study site), but was only 7%–10% of body weight in the winter. Froneman et al. (1996) found daily rations of 73% d⁻¹ in the ice-edge region of the Lazarev Sea. Huntley et al. (1989) estimated filtration rates of 4.1–9 L salp⁻¹ d⁻¹ for 40-mm salps near the Antarctic Peninsula, compared to our estimate of 13 L salp⁻¹ d⁻¹ (at warmer temperatures). Multiple studies have even estimated >100% of primary productivity consumed per day by salp communities (Dubischar and Bathmann 1997; Perissinotto et al. 1997; Bernard et al. 2012). However, these estimates have largely been based on only one or two net tows, rather than the extended sampling conducted during our Lagrangian experiments. Across the 23 bongo tows that we conducted during Cycle 1 (our longest Lagrangian study), calculated clearance rates on >10- μ m phytoplankton ranged from 1% of biomass consumed d⁻¹ for the tow with the lowest salp biomass to 30% d⁻¹ for the tow with the highest salp biomass. This tow-to-tow variability (driven by the inherent patchiness of salp populations) can thus lead to substantial over- or underestimation of average salp biomass and grazing pressure in a region if assessed from only a single tow. It is thus not surprising that our results (based on averaging 13–23 tows per cycle) fall near the mean range of prior estimates of salp grazing pressure.

One of the most important adaptations of pelagic tunicates is their fine feeding meshes that allow them to feed on organisms orders of magnitude smaller than themselves. Sutherland et al. (2010) has even suggested that *P. confederata* can satisfy its energetic requirements through ingestion of <1.4 μ m particles. Few studies, however, have directly quantified salp size-specific clearance rates on natural prey. Kremer and Madin (1992) found that *Pegea bicaudata* retention efficiencies were high for >2.5 μ m beads, but substantially lower for smaller beads, with the exception of the smallest (15 μ m) blastozoids assessed, which could feed efficiently on 1 μ m beads. For other species assessed (*P. confederata*, *S. aspera*, *Cyclosalpa polae*, and *Brooksia rostrata*), the authors found uniformly low retention efficiencies for 1 μ m beads regardless of salp length. Sutherland et al. (2010) found only slightly lower filtration rates for *P. confederata* on 0.5- and 1 μ m beads than on 3 μ m beads. Harbison and Gilmer (1976) found that *P. confederata* could feed on <1 μ m cultured cyanobacteria (*Coccolithis* sp.). Caron et al. (1989) found negligible filtration rates on *Synechococcus* (<1 μ m), moderate filtration rates on *Bodo* sp. (2–2.5 μ m) and high filtration rates on *Isochrysis galbana* (5 μ m) for *Cyclosalpa affinis*, *Salpa maxima*, and *P. confederata*.

Nishikawa and Tsuda (2001) quantified size-fractionated chlorophyll concentrations in salp grazing incubation experiments and concluded that salp grazing rates were highest on 2–20 μ m prey. Dadon-Pilosof et al. (2019) found substantially higher *S. maxima*, *Salpa fusiformis*, and *Thalia democratica* grazing rates on picoeukaryotes and nanoeukaryotes than on *Synechococcus*, *Prochlorococcus*, and heterotrophic bacteria. *Synechococcus* has also been found in the fecal pellets of salps (Pfannkuche and Lochte 1993), although this does not necessarily imply efficient feeding on cyanobacteria-sized cells, because mesozooplankton can also consume *Synechococcus* contained in aggregates (Stukel et al. 2013).

Our results are largely in line with these previous studies and show that *S. thompsoni* retention efficiency is lower when feeding on picoplankton than when feeding on nano- and microplankton. Our results do, however, show a distinct change in size selectivity with increasing size. The smallest blastozoids were able to feed efficiently on ~1 μ m cells and had reasonably high clearance rates even for 0.4 μ m cells. This gave them access to abundant picoplanktonic cells. Larger taxa (e.g., common 60-mm blastozoids or 100-mm oozoids), however, were only able to feed efficiently on nano- and microplankton cells. Despite differences in equivalent mesh diameter, our results suggest that the diets of differently sized salps were similar. Extensive flow cytometric analyses of samples from throughout the euphotic zone on each cycle (Fig. 3) showed that phytoplankton biomass was concentrated in the nano- and microphytoplankton size classes. All size classes of *S. thompsoni* thus derived the majority of their (phytoplankton) carbon from >8- μ m phytoplankton (which still yields a predator : prey length ratio of >10,000 : 1 for the largest oozoids). Small blastozoids, however, would have had much greater access to the biomass (5.9–37 μ g C L⁻¹) contained in heterotrophic bacteria in the mixed layer. For comparison, mean mixed layer eukaryotic phytoplankton biomass was 62, 88, and 101 μ g C L⁻¹, for Cycles 1, 2, and 4, respectively. Prokaryotes were thus likely to be an important source of nutrition for newly released blastozoids, although even for these small salps, the most important prey item was nano- and microphytoplankton.

Salp competitive interactions

In the Southern Ocean, *S. thompsoni* has often been considered a competitor of *E. superba*. The assumption of competitive interactions between these taxa stems, in part, from the fact that they are often the two dominant macrozooplankton species in the Southern Ocean, yet are commonly found in distinctly different water parcels (Pakhomov et al. 2002). Although some have hypothesized direct interactions between *E. superba* and *S. thompsoni* at various ontogenetic stages (Huntley et al. 1989), exploitation competition is most frequently invoked as the primary mode of interaction between the species; that is, salp grazing pressure exhausts the prey field necessary for successful *E. superba* feeding and vice versa

(Loeb et al. 1997). However, the two species may fill distinctly different niches. *E. superba* thrives in diatom-dominated regions (Haberman et al. 2003), and may supplement its diet via substantial carnivory on copepods and other taxa when microplankton are not abundant (Nordhausen et al. 1992; Cripps and Atkinson 2000). In contrast, *S. thompsoni* can feed on small phytoplankton and often excels in mesotrophic conditions (Zeldis et al. 1995; Pakhomov and Hunt 2017; Kelly et al. 2020). Indeed, our study shows that small *S. thompsoni* blastozooids can feed efficiently on cells as small as $1.2 \mu\text{m}$, while even large ($125 \mu\text{m}$) oozoids could feed efficiently on cells $> 4.7 \mu\text{m}$. Both groups derived over half of their (phytoplankton-based) nutrition from $< 10 \mu\text{m}$ cells that are largely unavailable to *E. superba* (although we note that *S. thompsoni* was likely deriving some nutrition from cells greater than our $30 \mu\text{m}$ cutoff, as well as cyanobacterial cells not assessed in this study). Blastozooids and oozoids also had the potential to derive substantial nutrition from even smaller cells if the phytoplankton community was dominated by picoplankton. These results suggest that salps and krill may not be direct competitors in the Southern Ocean. Rather, each flourishes in distinctly different conditions; krill during diatom blooms and salps in mesotrophic regions. Multiple studies have found that *S. thompsoni* abundances are often higher when Chl *a* concentrations are low (Pakhomov and Hunt 2017; Kelly et al. 2020). One explanation for the absence of *S. thompsoni* aggregations in diatom-dominated coastal regions is the potential for clogging of their feeding webs when plankton biomass is high (Harbison et al. 1986). Alternately, it is possible that *S. thompsoni* is hindered by low reproductive success in very cold waters (Henschke and Pakhomov 2019) or that the short ($< 1 \text{ yr}$) life span of *S. thompsoni* makes it poorly adapted to highly seasonal waters along the Antarctic continent where prey concentrations may be too low to sustain growth, and indeed substantially reduced feeding has been measured in winter in the Lazarev Sea (von Harbou et al. 2011).

Regardless, it appears that even when they are abundant, as in this study, salps seldom exert higher grazing pressure than protists and hence are unlikely to prevent *E. superba* growth through competitive exclusion. Indeed, although protistan communities typically exert greater grazing pressure on picophytoplankton than on diatoms, diatom mortality due to protistan grazing is substantial in many regions (Selph et al. 2001, 2011; Sherr and Sherr 2007) and protistan grazing pressure often has no clear dependence on phytoplankton size (Taniguchi et al. 2014). Furthermore, in this study we found no significant decline in protistan grazing on large ($30 \mu\text{m}$) phytoplankton relative to picophytoplankton, suggesting that protists (rather than *S. thompsoni*) may prevent microplankton blooms that would benefit *E. superba*. Conversely, *E. superba* does not feed efficiently on the nanoplankton that were the most important salp prey in our study, and hence are unlikely to exclude *S. thompsoni*. Instead, it is protistan grazers that

typically control pico- and nanophytoplankton biomass globally and in the Southern Ocean (Calbet and Landry 2004; Pearce et al. 2011; Latasa et al. 2014).

It thus may be more useful to assess competitive interactions between salps and protistan grazers. These organisms compete for similar prey items and both have life spans that can be similar to or shorter than the time scale of a Southern Ocean phytoplankton bloom. This allows both groups to respond reproductively to phytoplankton blooms. In fact, the ability of protists and salps to respond to increasing phytoplankton production may determine whether or not a bloom becomes too dense and causes salp mesh clogging (Harbison et al. 1986). Conversely, intense protistan grazing pressure has the potential to maintain phytoplankton biomass levels at concentrations too low for salps to consume sufficient carbon to satisfy their metabolic and growth requirements. It seems that in our study region, salp grazing rates (including consumption of heterotrophs and nonliving material) were likely high enough to slightly exceed their daily requirements. More effective protistan grazing control, however, could potentially lead to reduced phytoplankton standing stock and insufficient ingestion rates to support salp growth. Indeed, Cycle 5 (the “non-salp” cycle with lowest salp biomass) had lower Chl *a* than the other cycles. We thus consider it likely that competition with protistan grazers may be an important ecological interaction for *S. thompsoni*.

Additionally, with their nonselective grazing abilities, salps have the potential to exert important grazing pressure on protistan competitors. This is particularly interesting given the difference in grazing threshold between mature oozoids (i.e., feeding efficiently only on $> 5 \mu\text{m}$ cells) and the chains of small blastozooids that they release (which fed effectively on picoplankton in our study). It is possible that direct consumption of nano- and microzooplankton by mature oozoids relieves grazing pressure on picoplankton, thus stimulating net growth of a potential prey item for their offspring. In support of this hypothesis, Cycle 1 (our cycle with the highest abundance of large oozoids) also had the highest relative contribution of picoeukaryotic phytoplankton (Fig. 3). Although we did not detect reduced protistan grazing pressure on picophytoplankton during this cycle (Fig. 4), this may have been due to our occupation of the water parcel soon after the release of substantial numbers of young blastozooids (Fig. 2), whose grazing activity may have already impacted the protistan community before our arrival.

Given these expected interactions between protists and *S. thompsoni*, it is worth considering expected shifts that would occur in pelagic ecosystems if a protist-dominated grazer community shifted to a mixed protist-salp community. One of the most important ecological differences between salps and protists is vastly different predatory : prey size ratios. Protistan zooplankton typically feed with a predator : prey size ratio (linear dimension) of between 3 : 1 and 5 : 1 with some dinoflagellates exhibiting a lower ratio of 1 : 1 and ciliates

feeding at a 10 : 1 or higher size ratio (Sherr and Sherr 2007; Fuchs and Franks 2010; Dolan et al. 2013). In contrast, as shown here, *S. thompsoni* feeds at closer to a 10,000 : 1 predator : prey size ratio. This has profound implications for energy and matter transfer through food webs. Because of their high predator : prey size ratios, salps can efficiently shunt the productivity of pico- and nanophytoplankton carbon to larger nektonic predators (Henschke et al. 2016). Contrary to the prior assumption that salps (in contrast to euphausiids) were “trophic dead ends,” when compared to protist-dominated communities, salp blooms should substantially increase food availability to fish and other top predators, and indeed many of these higher trophic level species have been found to feed on them (Cardona et al. 2012; Henschke et al. 2016).

Salps also alter the biogeochemical functionality of pelagic ecosystems, relative to their protist competitors. Protist grazing enhances nutrient regeneration and dissolved organic matter production through the microbial loop (Steinberg and Landry 2017). Although some large protists can produce slowly sinking “mini” fecal pellets, it is generally safe to assume that the majority of the carbon and nitrogen consumed by protists will be recycled within the euphotic zone, with approximately 30% converted into protist biomass (Straile 1997). Most of this secondary production, however, will wind up being consumed by other links in the protistan food web, leading to only inefficient transfer to larger organisms (Landry and Calbet 2004). Salps, in contrast, produce rapidly sinking fecal pellets that can substantially increase particle flux out of the upper ocean (Madin 1982; Stone and Steinberg 2016). Their carcasses can also contribute substantially to export flux (Henschke et al. 2013; Smith et al. 2014). It thus seems likely that, while salp blooms may increase trophic efficiency and enhance transfer to top predators, they may also decrease the duration of phytoplankton blooms by reducing remineralization rates. This may increase the variability and patchiness in food supply in the pelagic ocean with unknown effects on other taxa.

Despite these hypotheses about pelagic food-web modifications in response to salp blooms, we caution that few studies have directly assessed the interactions between salps and protistan zooplankton. Understanding how Southern Ocean ecosystems will respond to a predicted southward expansion of *S. thompsoni* (Atkinson et al. 2004) thus requires answering key questions: Can salps exert top-down control on protistan zooplankton communities? How do the size spectra of ambient prey fields, salp clearance rates, and protistan clearance rates vary in time and space? Do salp and protistan zooplankton abundances and/or grazing impact covary in time and space? Do specific protistan taxa exhibit species-specific interactions with salps or their common prey items? How many trophic steps separate herbivorous protistan zooplankton from crustaceans and/or salps? What proportion of salp diets come from heterotrophic and/or mixotrophic protists? What is the

role of bacterivory by protists and salps in Southern Ocean food webs? Answering these questions will require coordinated studies by protistan and salp ecologists, but has the potential to transform our understanding of these diverse organisms and their changing ecosystem.

Conclusion

Our experimental design allowed us to quantify size-specific grazing rates for salps and protistan grazers during the evolution of a *S. thompsoni* bloom. Salp filtration rates and equivalent mesh size were size dependent: the smallest (6 mm) blastozoids had filtration rates of $\sim 0.2 \text{ L d}^{-1}$ and could efficiently feed on cells greater than $\sim 1\text{-}\mu\text{m}$ diameter, while the largest (150-mm) oozoids filtered $> 200 \text{ L d}^{-1}$ but could only efficiently retain cells greater than $\sim 6\text{-}\mu\text{m}$ diameter. These filtration rates, combined with high abundances at the beginning of the salp bloom, allowed the *S. thompsoni* community to clear $\sim 8\%$ of nano- and microphytoplankton biomass d^{-1} . Protistan zooplankton, however, were the dominant consumers of these prey items; daily, they consumed approximately 50% of all eukaryotic phytoplankton size classes (0.7–30 μm). This shows that protists are important competitors of salps despite the fact that these protists typically feed at less than a 10 : 1 predator : prey size ratio, while our results show that the salps were mostly feeding at a predator : prey size ratio between 1000 : 1 and 40,000 : 1.

References

- Atkinson, A., V. Siegel, E. Pakhomov, and P. Rothery. 2004. Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature* **432**: 100–103. doi:10.1038/nature02950
- Bernard, K. S., D. K. Steinberg, and O. M. E. Schofield. 2012. Summertime grazing impact of the dominant macrozooplankton off the Western Antarctic Peninsula. *Deep-Sea Res. I* **62**: 111–122. doi:10.1016/j.dsr.2011.12.015
- Bone, Q. 1998. The biology of pelagic tunicates. Oxford Univ. Press.
- Bradford, J. 1985. Distribution of zooplankton off Westland, New Zealand, June 1979 and February 1982. *New Zeal. J. Mar. Fresh. Res.* **19**: 311–326.
- Bruland, K. W., and M. W. Silver. 1981. Sinking rates of fecal pellets from gelatinous zooplankton (salps, pteropods, doliolids). *Mar. Biol.* **63**: 295–300.
- Calbet, A. 2008. The trophic roles of microzooplankton in marine systems. *ICES J. Mar. Sci.* **65**: 325–331. doi:10.1093/icesjms/fsn013
- Calbet, A., and M. R. Landry. 2004. Phytoplankton growth, microzooplankton grazing, and carbon cycling in marine systems. *Limnol. Oceanogr.* **49**: 51–57.
- Cardona, L., I. Álvarez de Quevedo, A. Borrell, and A. Aguilar. 2012. Massive consumption of gelatinous plankton by

- Mediterranean apex predators. PLoS One **7**: e31329. doi:[10.1371/journal.pone.0031329](https://doi.org/10.1371/journal.pone.0031329)
- Caron, D. A., P. D. Countway, A. C. Jones, D. Y. Kim, and A. Schnetzer. 2012. Marine protistan diversity. *Ann. Rev. Mar. Sci.* **4**: 467–493. doi:[10.1146/annurev-marine-120709-142802](https://doi.org/10.1146/annurev-marine-120709-142802)
- Caron, D. A., L. P. Madin, and J. J. Cole. 1989. Composition and degradation of salp fecal pellets: Implications for vertical flux in oceanic environments. *J. Mar. Res.* **47**: 829–850.
- Chiswell, S. M., J. Bradford-Grieve, M. G. Hadfield, and S. C. Kennan. 2013. Climatology of surface chlorophyll a, autumn-winter and spring blooms in the southwest Pacific Ocean. *J. Geophys. Res. Oceans* **118**: 1003–1018. doi:[10.1002/jgrc.20088](https://doi.org/10.1002/jgrc.20088)
- Cripps, G., and A. Atkinson. 2000. Fatty acid composition as an indicator of carnivory in Antarctic krill, *Euphausia superba*. *Can. J. Fish. Aquat. Sci.* **57**: 31–37.
- Dadon-Pilosof, A., F. Lombard, A. Genin, K. R. Sutherland, and G. Yahel. 2019. Prey taxonomy rather than size determines salp diets. *Limnol. Oceanogr.* **64**: 1996–2010. doi:[10.1002/lno.11165](https://doi.org/10.1002/lno.11165)
- Décima, M., M. R. Stukel, L. López-López, and M. R. Landry. 2019. The unique ecological role of pyrosomes in the Eastern Tropical Pacific. *Limnol. Oceanogr.* **64**: 728–743. doi:[10.1002/lno.11071](https://doi.org/10.1002/lno.11071)
- Dolan, J. R., D. J. S. Montagnes, S. Agatha, D. W. Coats, and D. K. Stoecker. 2013. The biology and ecology of tintinnid ciliates. Wiley-Blackwell.
- Dubischar, C. D., and U. V. Bathmann. 1997. Grazing impact of copepods and salps on phytoplankton in the Atlantic sector of the Southern Ocean. *Deep-Sea Res. II* **44**: 415–433.
- Froneman, P., E. Pakhomov, R. Perissinotto, and C. McQuaid. 1996. Role of microplankton in the diet and daily ration of Antarctic zooplankton species during austral summer. *Mar. Ecol. Prog. Ser.* **143**: 15–23.
- Fuchs, H. L., and P. J. S. Franks. 2010. Plankton community properties determined by nutrients and size-selective feeding. *Mar. Ecol. Prog. Ser.* **413**: 1–15.
- Garzio, L. M., D. K. Steinberg, M. Erickson, and H. W. Ducklow. 2013. Microzooplankton grazing along the Western Antarctic Peninsula. *Aquat. Microb. Ecol.* **70**: 215–232. doi:[10.3354/ame01655](https://doi.org/10.3354/ame01655)
- Gowing, M. 1989. Abundance and feeding ecology of Antarctic phaeodarian radiolarians. *Mar. Biol.* **103**: 107–118.
- Haberman, K. L., R. M. Ross, and L. B. Quetin. 2003. Diet of the Antarctic krill (*Euphausia superba* Dana): II. Selective grazing in mixed phytoplankton assemblages. *J. Exp. Mar. Biol. Ecol.* **283**: 97–113.
- Hansen, P. J., P. K. Bjornsen, and B. W. Hansen. 1997. Zooplankton grazing and growth: Scaling within the 2–2,000- μ m body size range. *Limnol. Oceanogr.* **42**: 687–704.
- Harbison, G. R., and R. W. Gilmer. 1976. The feeding rates of the pelagic tunicate *Pegea confederata* and two other salps. *Limnol. Oceanogr.* **21**: 517–528.
- Harbison, G. R., V. L. McAlister, and R. W. Gilmer. 1986. The response of the salp, *Pegea confoederata*, to high levels of particulate material: Starvation in the midst of plenty. *Limnol. Oceanogr.* **31**: 371–382.
- Henschke, N., and others. 2013. Salp-falls in the Tasman Sea: A major food input to deep-sea benthos. *Mar. Ecol. Prog. Ser.* **491**: 165–175.
- Henschke, N., J. D. Everett, A. J. Richardson, and I. M. Suthers. 2016. Rethinking the role of salps in the ocean. *Trends Ecol. Evol.* **31**: 720–733.
- Henschke, N., and E. A. Pakhomov. 2019. Latitudinal variations in *Salpa thompsoni* reproductive fitness. *Limnol. Oceanogr.* **64**: 572–584.
- Huntley, M. E., P. F. Sykes, and V. Marin. 1989. Biometry and trophodynamics of *Salpa thompsoni* Foxton (Tunicata: Thaliacea) near the Antarctic Peninsula in austral summer, 1983–1984. *Polar Biol.* **10**: 59–70.
- Iguchi, N., and T. Ikeda. 2004. Metabolism and elemental composition of aggregate and solitary forms of *Salpa thompsoni* (Tunicata: Thaliacea) in waters off the Antarctic Peninsula during austral summer 1999. *J. Plankton Res.* **26**: 1025–1037.
- Kelly, P., and others. 2020. *Salpa thompsoni* in the Indian Sector of the Southern Ocean: Environmental drivers and life history parameters. *Deep-Sea Res. II* **174**: 104789.
- Kremer, P., and L. P. Madin. 1992. Particle retention efficiency of salps. *J. Plankton Res.* **14**: 1009–1015. doi:[10.1093/plankt/14.7.1009](https://doi.org/10.1093/plankt/14.7.1009)
- Lancraft, T. M., T. L. Hopkins, J. J. Torres, and J. Donnelly. 1991. Oceanic micronektonic/macrozooplanktonic community structure and feeding in ice covered Antarctic waters during the winter (AMERIEZ 1988). *Polar Biol.* **11**: 157–167.
- Landry, M. R., and A. Calbet. 2004. Microzooplankton production in the oceans. *ICES J. Mar. Sci.* **61**: 501–507.
- Landry, M. R., L. W. Haas, and V. L. Fagerness. 1984. Dynamics of microbial plankton communities: Experiments in Kaneohe Bay, Hawaii. *Mar. Ecol. Prog. Ser.* **16**: 127–133.
- Landry, M. R., M. D. Ohman, R. Goericke, M. R. Stukel, and K. Tsyrklevich. 2009. Lagrangian studies of phytoplankton growth and grazing relationships in a coastal upwelling ecosystem off Southern California. *Prog. Oceanogr.* **83**: 208–216. doi:[10.1016/j.pocean.2009.07.026](https://doi.org/10.1016/j.pocean.2009.07.026)
- Landry, M. R., M. R. Stukel, and M. Décima. 2020. Food-web fluxes support high rates of mesozooplankton respiration and production in the equatorial Pacific. *Mar. Ecol. Prog. Ser.* **652**: 15–32.
- Latasa, M., J. Henjes, R. Scharek, P. Assmy, R. Rottgers, and V. Smetacek. 2014. Progressive decoupling between phytoplankton growth and microzooplankton grazing during an iron-induced phytoplankton bloom in the Southern Ocean

- (EIFEX). Mar. Ecol. Prog. Ser. **513**: 39–50. doi:[10.3354/meps10937](https://doi.org/10.3354/meps10937)
- Loeb, V., V. Siegel, O. Holm-Hansen, and R. Hewitt. 1997. Effects of sea-ice extent and krill or salp dominance on the Antarctic food web. *Nature* **387**: 897.
- Lüskow, F., E. A. Pakhomov, M. R. Stukel, and M. Décima. 2020. Biology of *Salpa thompsoni* at the Chatham Rise, New Zealand: Demography, growth, and diel vertical migration. *Mar. Biol.* **167**: 175.
- Madin, L., and C. Cetta. 1984. The use of gut fluorescence to estimate grazing by oceanic salps. *J. Plankton Res.* **6**: 475–492.
- Madin, L., P. Kremer, P. Wiebe, J. Purcell, E. Horgan, and D. Nemazie. 2006. Periodic swarms of the salp *Salpa aspera* in the slope water off the NE United States: Biovolume, vertical migration, grazing, and vertical flux. *Deep-Sea Res. I* **53**: 804–819.
- Madin, L. P. 1982. Production, composition, and sedimentation of salp fecal pellets in oceanic waters. *Mar. Biol.* **67**: 39–45.
- Madin, L. P., and G. R. Harbison. 1977. The associations of Amphipod Hyperiidea with gelatinous zooplankton – I. Associations with Saplidae. *Deep Sea Res.* **24**: 449–463. doi:[10.1016/0146-6291\(77\)90483-0](https://doi.org/10.1016/0146-6291(77)90483-0)
- Madin, L. P., and J. E. Purcell. 1992. Feeding, metabolism, and growth of *Cyclosalpa bakeri* in the subarctic Pacific. *Limnol. Oceanogr.* **37**: 1236–1251.
- Menden-Deuer, S., and E. J. Lessard. 2000. Carbon to volume relationships for dinoflagellates, diatoms, and other protist plankton. *Limnol. Oceanogr.* **45**: 569–579.
- Nishikawa, J., and A. Tsuda. 2001. Feeding of the pelagic tunicate, *Salpa thompsoni*, on flagellates and size-fractionated chlorophyll particles. *Plankton Biol. Ecol.* **48**: 133–135.
- Nordhausen, W., M. Huntley, and M. D. G. Lopez. 1992. RACER: Carnivory by *Euphausia superba* during the antarctic winter. *Antarct. J. US* **27**: 181–183.
- Pakhomov, E. 2000. Demography and life cycle of Antarctic krill, *Euphausia superba*, in the Indian sector of the Southern Ocean: Long-term comparison between coastal and open-ocean regions. *Can. J. Fish. Aquat. Sci.* **57**: 68–90.
- Pakhomov, E., C. Dubischar, V. Strass, M. Brichta, and U. Bathmann. 2006. The tunicate *Salpa thompsoni* ecology in the Southern Ocean. I. Distribution, biomass, demography and feeding ecophysiology. *Mar. Biol.* **149**: 609–623.
- Pakhomov, E. A., P. W. Froneman, and R. Perissinotto. 2002. Salp/krill interactions in the Southern Ocean: Spatial segregation and implications for the carbon flux. *Deep-Sea Res. II* **49**: 1881–1907. doi:[10.1016/S0967-0645\(02\)00017-6](https://doi.org/10.1016/S0967-0645(02)00017-6)
- Pakhomov, E. A., and B. P. Hunt. 2017. Trans-Atlantic variability in ecology of the pelagic tunicate *Salpa thompsoni* near the Antarctic polar front. *Deep-Sea Res. II* **138**: 126–140.
- Pearce, I., A. T. Davidson, P. G. Thomson, S. Wright, and R. van den Enden. 2011. Marine microbial ecology in the sub-Antarctic zone: Rates of bacterial and phytoplankton growth and grazing by heterotrophic protists. *Deep-Sea Res. II* **58**: 2248–2259. doi:[10.1016/j.dsr2.2011.05.030](https://doi.org/10.1016/j.dsr2.2011.05.030)
- Perissinotto, R., E. Pakhomov, C. McQuaid, and P. Froneman. 1997. In situ grazing rates and daily ration of Antarctic krill *Euphausia superba* feeding on phytoplankton at the Antarctic polar front and the marginal ice zone. *Mar. Ecol. Prog. Ser.* **160**: 77–91.
- Pfannkuche, O., and K. Lochte. 1993. Open ocean pelago-benthic coupling: Cyanobacteria as tracers of sedimenting salp feces. *Deep-Sea Res. I* **40**: 727–737.
- Saba, G. K., and others. 2014. Winter and spring controls on the summer food web of the coastal West Antarctic peninsula. *Nature Comm.* **5**: 1–8. doi:[10.1038/ncomms5318](https://doi.org/10.1038/ncomms5318)
- Selph, K. E., M. R. Landry, C. B. Allen, A. Calbet, S. Christensen, and R. R. Bidigare. 2001. Microbial community composition and growth dynamics in the Antarctic polar front and seasonal ice zone during late spring 1997. *Deep-Sea Res. II* **48**: 4059–4080. doi:[10.1016/S0967-0645\(01\)00077-7](https://doi.org/10.1016/S0967-0645(01)00077-7)
- Selph, K. E., and others. 2011. Spatially-resolved taxon-specific phytoplankton production and grazing dynamics in relation to iron distributions in the equatorial Pacific between 110 and 140°W. *Deep-Sea Res. II* **58**: 358–377. doi:[10.1016/j.dsr2.2010.08.014](https://doi.org/10.1016/j.dsr2.2010.08.014)
- Sherr, E. B., and B. F. Sherr. 1994. Bacterivory and herbivory – key roles of phagotrophic protists in pelagic food webs. *Microb. Ecol.* **28**: 223–235.
- Sherr, E. B., and B. F. Sherr. 2007. Heterotrophic dinoflagellates: A significant component of microzooplankton biomass and major grazers of diatoms in the sea. *Mar. Ecol. Prog. Ser.* **352**: 187–197. doi:[10.3354/meps07161](https://doi.org/10.3354/meps07161)
- Smith, K. L., Jr., and others. 2014. Large salp bloom export from the upper ocean and benthic community response in the abyssal northeast Pacific: Day to week resolution. *Limnol. Oceanogr.* **59**: 745–757. doi:[10.4319/lo.2014.59.3.0745](https://doi.org/10.4319/lo.2014.59.3.0745)
- Spiegelhalter, D. J., N. G. Best, B. P. Carlin, and A. Van Der Linde. 2002. Bayesian measures of model complexity and fit. *J. R. Stat. Soc. Series B Stat. Methodology* **64**: 583–639.
- Steinberg, D. K., and M. R. Landry. 2017. Zooplankton and the ocean carbon cycle. *Ann. Rev. Mar. Sci.* **9**: 413–444.
- Stone, J. P., and D. K. Steinberg. 2016. Salp contributions to vertical carbon flux in the Sargasso Sea. *Deep-Sea Res. I* **113**: 90–100. doi:[10.1016/j.dsr.2016.04.007](https://doi.org/10.1016/j.dsr.2016.04.007)
- Straile, D. 1997. Gross growth efficiencies of protozoan and metazoan zooplankton and their dependence on food concentration, predator-prey weight ratio, and taxonomic group. *Limnol. Oceanogr.* **42**: 1375–1385.
- Strickland, J. D., and T. R. Parsons. 1972. A practical handbook of seawater analysis, second ed. Fisheries Research Board of Canada, Bulletin 167.

- Stukel, M. R., M. Décima, K. E. Selph, D. A. A. Taniguchi, and M. R. Landry. 2013. The role of *Synechococcus* in vertical flux in the Costa Rica upwelling dome. *Prog. Oceanogr.* **112-113**: 49–59. doi:[10.1016/j.pocean.2013.04.003](https://doi.org/10.1016/j.pocean.2013.04.003)
- Sutherland, K. R., L. P. Madin, and R. Stocker. 2010. Filtration of submicrometer particles by pelagic tunicates. *Proc. Natl. Acad. Sci. USA* **107**: 15129–15134.
- Sutton, P. 2001. Detailed structure of the subtropical front over Chatham rise, east of New Zealand. *J. Geophys. Res. Oceans* **106**: 31045–31056.
- Taniguchi, D. A. A., M. R. Landry, P. J. S. Franks, and K. E. Selph. 2014. Size-specific growth and grazing rates for picophytoplankton in coastal and oceanic regions of the eastern Pacific. *Mar. Ecol. Prog. Ser.* **509**: 87–101. doi:[10.3354/meps10895](https://doi.org/10.3354/meps10895)
- von Harbou, L., C. D. Dubischar, E. A. Pakhomov, B. P. Hunt, W. Hagen, and U. V. Bathmann. 2011. Salps in the Lazarev Sea, Southern Ocean: I. Feeding dynamics. *Mar. Biol.* **158**: 2009–2026.
- Zeldis, J. R., C. S. Davis, M. R. James, S. L. Ballara, W. E. Booth, and F. H. Chang. 1995. Salp grazing: Effects on phytoplankton abundance, vertical distribution and taxonomic composition in a coastal habitat. *Mar. Ecol. Prog. Ser.* **126**: 267–283.
- Zeldis, J. R., and M. Décima. 2020. Mesozooplankton connect the microbial food web to higher trophic levels and vertical

export in the New Zealand subtropical convergence zone. *Deep-Sea Res. I* **155**: 103146.

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Conflict of Interest

The authors declared no potential conflict of interest.

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