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Size and stage specific patterns in *Salpa thompsoni* vertical migration

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Abstract:

Vertical distribution and size-dependent migrations of the pelagic tunicate Salpa thompsoni were studied during late summer to early autumn (26th February – 15th March 2018) at contrasting hydrological stations over the Kerguelen Plateau (Southern Indian Ocean). Vertical migrators, such as S. thompsoni, have potentially significant impacts on the biological pump because of their large swarms, high grazing/fecal pellet production rates and extensive vertical migrations. S. thompsoni were undergoing diel vertical migration from a daytime weighted mean depth of ~450 m to a night time weighted mean depth of ~100 m. Smaller blastozooids and oozoids were the strongest vertical migrators, while their larger counterparts did not show a consistent diel cycle in their vertical distribution. Strong vertical migrations of the smallest blastozooids and oozoids imply high predation pressure on these groups. This knowledge has implications in modelling salp contributions to the vertical passive and active carbon fluxes.

Highlights

► This is the first study of size-dependent vertical migration of *Salpa thompsoni*. ► *Salpa thompsoni* were undergoing diel vertical migration between 450 and 100 m. ► Smaller individuals were the strongest migrators implying higher predation pressure. ► There was no consistent cycle in vertical distribution for large individuals. ► Understanding migration patterns has implications in carbon flux modelling.

Keywords: alp, Diel vertical migration, Southern ocean, Salpa thompsoni, Kerguelen Plateau

Introduction

The pelagic tunicate Salpa thompsoni is a successful zooplankton grazer found over a broad thermal (- 1.5 to 8 °C) and latitudinal range (40 – 65 °S) across the Southern Ocean (Foxton, 1966, Henschke and Pakhomov, 2018). Unlike its horizontal distribution, the vertical distribution and behavior of S. thompsoni is less well known, yet they have been sampled at a maximum depth of 1500 m (Foxton, 1966, Pakhomov et al., 2011). Several studies have documented strong diel vertical migration of S. thompsoni in the top 800 m layer, with the majority of salps concentrating near the surface during the darkness and between 200-600 m during the daytime (e.g., Casareto and Nemoto, 1986, Lancraft et al., 1989, Perissinotto and Pakhomov 1998, Nishikawa and Tsuda, 2001, Parker et al., 2015, Conroy et al., 2020) Their migration is closely linked to differences in the vertical distribution of blastozooic's ard oozooids during the salp life cycle (Foxton, 1966, Lancraft et al., 1991). Salps have a complex reproductive cycle that involves the obligatory alternation of sexual (blastozooia, and asexual (oozoid) generations. Oozoids are known to inhabit mesopelagic layers, or it cularly during the austral winter (Foxton, 1966). They are released in long chains by the surface oozoid generation. Upon release, female blastozooids need to be fertilized by older n. e blastozooids (Foxton, 1966). Therefore, some form of synchronized swarming should occur to allow successful reproduction. This has previously been observed in another salp species *Thalia democratica*, which synchronized reproduction in surface waters at 1. ght by forming large swarms (Heron, 1972).

While salp vertical distribution. Las been frequently documented, there are only a few studies that have specifically investional diel migration of *S. thompsoni*. There is evidence that *S. thompsoni* may alter its diel migration patterns to take advantage of phytoplankton rich surface layers (Nishikawa and Tsuda, 2001, Pakhomov et al., 2011) or avoid water masses outside their tolerance levels (Lancraft et al., 1989, 1991; Pakhomov, 1994; Pakhomov et al., 2011). It has been hypothesized that strong temperature gradients between warm and cold water layers in the Southern Ocean may halt the vertical movement of some small sized salps leading to a clear bimodal daytime vertical distribution of populations (Casareto and Nemoto, 1986, Lancraft et al., 1989, Pakhomov, 1993, 1994). The recent study conducted over the Chatham Rise east of New Zealand for the first time documented size-specific *S. thompsoni* vertical migration patterns (Lüskow et al. 2020).

Vertical migrators are increasingly important to biogeochemical cycling, particularly for species such as *S. thompsoni* that have potentially significant impacts on the biological pump because of their large swarms, high grazing/fecal pellet production rates and extensive vertical migrations (Bruland and Silver, 1981; Perissinotto and Pakhomov, 1998; Manno et al., 2015). If salps are migrating to the surface for both feeding and reproduction, a higher proportion of very large, reproducing salps, and very small, recently released salps should be evident in the size and stage distribution of the population in the same depth stratum. A better understanding of the size-specific migration patterns would improve active carbon transport estimates that are generally based on size. Here we explore the size and stage structured vertical distribution of *S. thompsoni* over the Kerguelen Plateau.

1 Methods

- 2 Salpa thompsoni sampling was undertaken on the RV Marion Dufresne II at four stations near
- 3 and on the Kerguelen Plateau during the "Marine Ecosystem Biodiversity and Dynamics of Car-
- 4 bon around Kerguelen: an integrated view" (MOBYDICK) expedition between February 26 and
- 5 March 19, 2018 (Fig. 1). This voyage was a continuation of three previous programs in the area,
- 6 with stations chosen to coincide with previously sampled areas. For more details on the sampling
- 7 design and population demographics of *Salpa thompsoni* from this study see Henschke et al.
- 8 (2021). The Kerguelen Plateau region has the largest seasonal phytoplankton blooms of any
- 9 Southern Ocean island systems (Blain et al., 2007) and is an important feeding ground for fish
- 10 populations and top predators (Guinet et al., 1996; Cherel et al., 1905). At each station, daytime
- 11 (0700-1400) and nighttime (1900-0200) trawls were cord cte-l using the Mesopelagos trawl
- 12 (Meillat, 2012) in surface (50 100 m), middle (200 650 m) and deep (300 800 m) layers
- 13 (Table 1; Table S1). Due to the large mesh size in the trav. these samples may consistently un-
- 14 derestimate individuals smaller than 25 mm, howe ver, as small blastozooids generally occur in
- chains the undersampling is likely to mostly ""fect small oozoids which comprised 3% of sam-
- 16 ples (Henschke et al. 2021). Corresponding, at each station, hydrographic characteristics were
- sampled with a SeaBird SBE 19+ Conductivity-Temperature-Depth (CTD) probe equipped with
- 18 a calibrated Chelsea Aqua-Tracker Mx? 1 uorometer.

19

- 20 S. thompsoni individuals were exact into oozoids or blastozooids, measured for the oral-atrial
- body length (OAL) and their modurity stage identified (Foxton, 1966). Oozoids (stages 0-3) are
- 22 reproductively immature until the development and release of blastozooid buds (stage 4
- onwards). Blastozooids $\$ gin as reproductively immature females (stage 0-3). Once
- 24 reproductive, they release an oozoid embryo at stage 4, and then develop testis and function as a
- 25 male (stage M). Results across stations were pooled in this study to explore the general trends in
- vertical distribution. For more details on sampling methods and *S. thompsoni* population
- 27 dynamics see Henschke et al. (2021).

28

29 The weighted mean depth (WMD, m) of the *Salpa thompsoni* population was calculated:

$$WMD = \frac{\sum (a_i \cdot d_i)}{\sum a_i}$$

30	where a_i is the abundance of <i>S. thompsoni</i> (ind. m ⁻³) and d_i is the midpoint of the depth stratum
31	in each sampling location i .
32	
33	To determine size-specific migration, blastozooids and oozoids were binned into 1 and 5 mm
34	size intervals respectively before calculating the night/day abundance ratios in deep (300 - 600 $$
35	m) layers. A ratio greater than 1 indicates higher proportions of that size class occurring at that
36	respective depth (surface or deep) at night time. This ratio was not calculated at other depths as it
37	requires both day and night size distributions; daytime distributions were mostly absent in
38	surface water $(0 - 100 \text{ m})$.

39 **Results** 40 Salpa thompsoni were sampled down to depths of 814 m during the day and 802 m at night. 41 Depth integrated night time abundance was significantly greater than daytime abundances ($F_{1,31}$ = 6.08, p = 0.02). Blastozooids (15.55 \pm 24.86 individuals (ind.) 1000 m⁻³) and oozoids (10.26 \pm 42 14.24 ind. 1000 m⁻³) were approximately 20-fold more abundant during the night than during the 43 day (blastozooid: 0.48 ± 0.85 ind. 1000 m^{-3} ; oozoid: 0.94 ± 1.19 ind. 1000 m^{-3}). 44 45 46 Blastozooids and oozoids both displayed pronounced diel vertical migration, with weighted mean depths much deeper during the day (blastozooids: 449 m, oozcids: 465 m) than at night 47 48 (blastozooids: 87 m, oozoids: 115 m; Fig. 2). Blastozooids were beent above 300 m during the 49 day, whereas a small proportion (10%) of large, reproductive pozpids (77 - 89 cm) were present. 50 Juvenile females (10 - 25 mm; Table 2) made up the majority of the blastozooid population in 51 surface waters (0 - 100 m) at night (Fig. 3a). In degree layers (300 - 600 m), juvenile females 52 were more dominant during the day, showing similar size distribution to the night time surface 53 54 samples, whereas larger blastozooids becan more dominant at night (Fig. 3c). At night reproducing females and males were 20 > 40 times more abundant in deeper water (300 - 600)55 56 m; Fig. 3e; Table 2). 57 58 In general, the size distribution of pozoids were more evenly distributed in surface water (Fig. 59 3b), with peaks in juvenile and approducing oozoids (Table 2). Reproductively immature individuals (< 50 mm; Fauly 2) made up the largest proportion of oozoids during the day in deep 60 61 water (Fig. 3c), whereas "he night time distribution was characterized by higher proportions of 62 reproducing individuals (50-75 mm). Reproducing individuals also made up the largest change 63 in density; 10 - 20 times more abundant at night than during the day in deep water (Fig. 3f). 64 65

Discussion 66 67 Salpa thompsoni populations on the Kerguelen Plateau were undergoing diel vertical migration 68 from a daytime weighted mean depth of ~ 450 m to a night time weighted mean depth of ~ 100 69 m. This pattern had been well documented during previous studies and salps often have been 70 observed visually near the surface at night (Casareto and Nemoto, 1986, Lancraft et al., 1989, 71 Krakatitsa et al., 1993, Perissinotto and Pakhomov 1998, Conroy et al., 2020). In our study, the 72 highest nighttime abundances indeed occurred in the top 100 m, which corresponded with the 73 chlorophyll a maximum. This suggests that, like in other parts of the Southern Ocean, the S. 74 thompsoni population was migrating to take advantage of the food-1. h surface layers 75 (Nishikawa and Tsuda 2001, Pakhomov et al., 2011). While the vho e population was performing diel-vertical migration, this migration varied depending on S. thompsoni size and 76 77 stage. Blastozooids and oozoids were absent in the top 300 m during the day time, with the exception of a small proportion of very large, reproducing pozoids. Residing in surface waters 78 during the day time may expose salps to visual predeces, with midwater fish, seabirds and seals 79 80 suggested to be potential consumers (Pakhor...v + al., 2002, Henschke et al. 2016). Midwater fish are nocturnal feeders and generally pre, on small salp individuals (Saunders et al., 2019). 81 82 Hence, the main potential predators for u. a large oozoids would be seabirds and seals; however 83 observations of penguin or seal predation are rare (Thiebot and McInnes, 2019). If the large 84 oozoids in this study avoided the par-surface layers (0 - 30 m), they may circumvent daytime 85 predation from seabirds but not diving penguins or seals. Oozoids of this size (80 - 90 mm) 86 would be producing up to 2 chains of 250 identical blastozooid buds (Daponte et al. 2001), 87 which would require a .ig. if cant amount of energy (Henschke et al. 2018). Hence, it is plausible 88 that reproducing oozoids are choosing to remain in the food-rich surface layers during the day 89 time to maximize their energy intake for reproduction. 90 91 Juvenile blastozooids (10 - 25 mm) migrated into surface waters during the night from daytime 92 depths between 300 – 600 m. This was observed in the Pacific Sector of the subantarctic region 93 (Lüskow et al. 2020). Correspondingly, juvenile oozoids (20 - 60 mm) also migrated into surface 94 water at night time. Such behavior clearly suggests that small to medium sized blastozooids and oozoids were major contributors to the population's vertical migrations into the surface water. 95

Interestingly, the majority of blastozooid and oozoid size clases were at least 2 times more
abundant at night at 300-600 m, suggesting their daytime residence at much deeper layers.
Larger and mature blastozooids (25 - 32 and 44 - 52 mm) and oozoids (60 - 75 mm) were $10-$
40 times more abundant at night in deep water. This concurs with previous findings that embryo
(young oozoid) release may occur below the euphotic zone (Foxton, 1966, Casareto and Nemoto
1986). Nevertheless, this phenomenon requires further investigation because the largest
blastozooids are likely all functional males and currently we do not know when the egg
fertilization in young blastozooids occurs. Previously, it has been proposed that chain release
mainly occurs near the surface (Foxton, 1966). Therefore, active migration of small to medium
blastozooids would be ecologically justified because they are the most actively growing
specimens that could be under heavy predation pressure. We fid abserve the smallest
blastozooids (≤ 10 mm) in deeper layers at nighttime, al¹ crung us to hypothesize that chain
release may also occasionally occur below the euphotic zeroe, which corresponds with higher
proportions of larger reproductive oozoids display $n_{\mathcal{S}}$ ϵ deeper daytime residence. This however
requires confirmation because it could also by an artifact of sample contamination during trawl
deployment (Henschke et al., 2021).
The higher night time proportions of .a' ge1 blastozooids and oozoids at depths 300 - 600 m, and
their weighted mean depth of ~450 m, implies that large size classes of Salpa thompsoni may be
migrating from even deeper lagers. In this study they were found to 800 m during the day, albeit
in low abundances. During the current study, the deepest sampling events were rare (2 out of 47
trawls), with the major versampling (47 %) undertaken in the top 300 m. A more detailed
sampling program is required to explore the maximum depth distribution and residency of
various stages and sizes of S . $thompsoni$. However, depth-integrated night time salp abundances
were ~ 20 times greater than daytime abundances. While the deepest sampling depths in this
study could be misrepresented due to lower sample sizes, sampling effort at each depth was
similar between day and night further suggesting that the daytime residence of S. thompsoni
could be below 800 m. In this study, tows were targeting high backscattering signals, hence it is
possible that target tows missed layers with high salp densities because they may have been
acoustically invisible. At one station there were strong patches migrating at mid-day from ~ 200
m depth to the surface (Fig. S1), which could correspond to S. thompsoni as they have been

128	found to migrate upward when solar radiation is at its strongest (Nishikawa and Tsuda, 2001).
129	More detailed analysis on the ability to detect S. thompsoni in acoustic backscattering layers is
130	needed to elucidate this theory.
131	
132	In summary, smaller blastozooids and oozoids were the strongest vertical migrators, while their
133	larger counterparts may have either a longer, or/and deeper migration cycle; but this is still
134	poorly understood. Strong vertical migrations of the smallest blastozooids and oozoids could
135	imply high predation pressure on these groups and thus their importance to higher trophic levels.
136	It has been postulated that the intensity of salp vertical migrations in v be dictated by the salp
137	size (Lüskow et al. 2020). This knowledge is critical, particularly in nodelling salp contributions
138	to the vertical passive and active carbon fluxes.
139	
140	

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142	
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Table 1. Count of trawls (n) undertaken in each depth layer. For more detail on station specific trawl data see supplementary information.

	Day		Night	
Depth layer (m)	Average depth (m)	n	Average depth (m)	n
0-100	70	6	66	9
100-200	155	3	167	2
200-300	210	1	290	1
300-400	347	3	368	5
400-500	424	4	415	1
500-600	588	2	583	2
600-700	642	3	626	3
700-800	814	1	802	1

241 Table 2. Mean size of Salpa thompsoni blastozooid and oozoid stages from this study

Blastozoo	id		Oozoid					
Stage	Mean size (mm)	n	Stage	Mean size (mm)	n			
0	13.21	509	0	5.40	7			
1	17.51	291	1	19.46	16			
2	22.65	539	2	25.43	102			
3	26.06	80	3	3.1.36	203			
4	31.34	5	4	52.18	244			
5	36.73	338	45	65.91	106			
6	22.63	333	5	80.68	55			
			5.5	89.66	35			

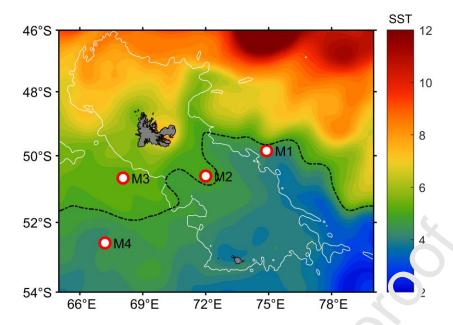


Figure 1. Map of stations sampled during the MOBYDICK expedition, from 26 February to 19 March 2018 with average sea surface temperature (SSL) overlaid. Dashed line represents the 5 degree isotherm. SST data were retrieved using the Copernicus platform (http://marine.copernicus.eu). Data were produced by running the OSTIA system, a merged, multi-sensor L4 Foundation SST product, with a spatial resolution of 0.05 degrees (Donlon et al. 2012). The continental slope (continuous white line, 1000 m isobath) and the Polar Front (dashed black line, 5°C SST) are represented.

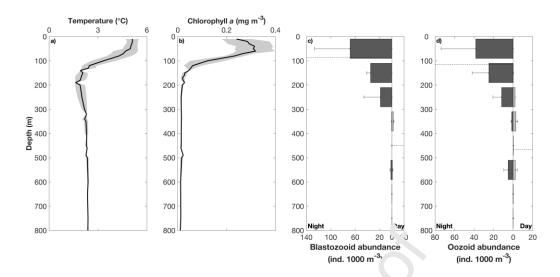


Figure 2. Mean (\pm SD) temperature (a), chlorophyll *a* biomas. (b) and mean (\pm SE) day/night vertical distribution of *Salpa thompsoni* blastozooids (c) and pozoids (d). Dashed lines in c-d indicate weighted mean depth.

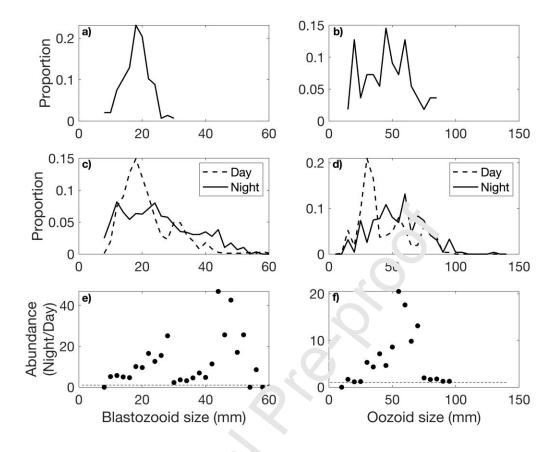


Figure 3. Proportional size distribution of *Salpa thompsoni* blastozooids (a, c) and oozoids (b, d) in the surface (0 - 1.00 m); top row) and deep (300 - 600 m); middle row) layer. Blastozooids and oozoids were only sampled during the night in surface water so there are no daytime values. Hence the Night/Day abundance ratio of blastozooids (e) and oozoids (f) by size bin in only availabile for the deep layer.

Supplementary Information

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Table S1. Sampling location, dates and maximum depths for trawls. Trawl depth varied slightly depending on oceanographic conditions and the ability to hold the targeted depth, however, targeted depth was usually within ~ 10 m of the maximum depth. NS – no sample. Table from Henschke et al. (2021)

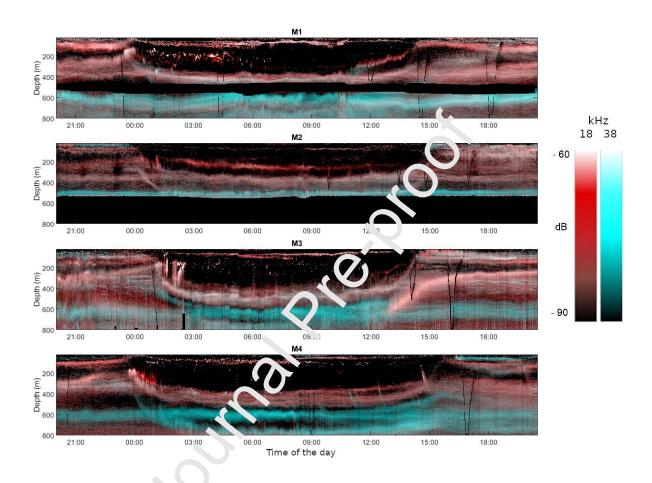
Site	Location	Visit	Sampling date	Day/	Sampling	Visit	Sampling date	Day/	Sampling	Visit	Sampling date	Day/	Sampli
	(°S, °E)		(DD/MM/YY)	Night	depth (m)		(DD/MM/YY)	N'.gı.	depth (m)		(DD/MM/YY)	Night	depth (
M1	49.85,	1	09/03/18	D	400				•				
	74.90			D	50								
				D	632								
				N	51								
				N	290								
				N	617								
M2	50.62,	1	26/02/18 -	D	NS	?.	ე7/03/18	D	170	3	16/03/18 -	D	105
	72.00		27/02/18	D	210			D	70		17/03/18	D	340
				D	350			D	350			D	190
				N	3+6			N	317			N	65
				N	5.			N	50			N	377
				N	158			N	175			N	30
M3	50.68,	1	4/03/18*,	7)	55*	2	18/03/18 -	D	814				
	68.06		15/03/18	Г	460*		19/03/18	D	600				
				D	683			D	65				
				N	610			N	802				
				N	90			N	650				
				N	415			N	73				
M4	52.60,	1	01/03/18 -	D	93	2	14/03/18	D	85				
	67.20		02/03/18	D	575			D	610				
				D	425			D	410				
				N	400			N	600				

N	96	N	80
N	575	N	400

* M3 visit 1 had to be performed over two separate visits due to bad weather. The first two-day sampling events occurred on 4/3/18, whereas the

remaining day and night events occurred on 15/03/18.

Supplementary Figure 1. Daily RGB composites of Sv values (dB re.1m⁻¹) from 12 to 800m for the four stations, with the 18 kHz displayed in red and 38 kHz frequency displayed both in green and blue. Figure from Cotte et al. (2021).



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Highlights

- This is the first study of size-dependent vertical migration of Salpa thompsoni
- *Salpa thompsoni* were undergoing diel vertical migration between 450 100 m.
- Smaller individuals were the strongest migrators implying higher predation pressure.
- There was no consistence cycle in vertical distribution for large individuals.
- Understanding migration patterns has implications in carbon flux modelling.