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► **To cite this version:**

Natasha Henschke, Yves Cherel, Cédric Cotté, Boris Espinasse, Brian P.V. Hunt, et al.. Size and stage specific patterns in *Salpa thompsoni* vertical migration. *Journal of Marine Systems*, 2021, 222, pp.103587. 10.1016/j.jmarsys.2021.103587 . hal-03247806

HAL Id: hal-03247806

<https://hal.science/hal-03247806>

Submitted on 15 Aug 2023

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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 blastozoids 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 blastozoids 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 blastozooids and oozoids during the salp life cycle (Foxton, 1966, Lancraft et al., 1991). Salps have a complex reproductive cycle that involves the obligatory alternation of sexual (blastozooid) and asexual (oozoid) generations. Oozoids are known to inhabit mesopelagic layers, particularly 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 male 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 night by forming large swarms (Heron, 1972).

While salp vertical distribution has been frequently documented, there are only a few studies that have specifically investigated 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., 2005). At each station, daytime
11 (0700 – 1400) and nighttime (1900 – 0200) trawls were conducted 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 trawl, these samples may consistently un-
14 derestimate individuals smaller than 25 mm, however, as small blastozooids generally occur in
15 chains the undersampling is likely to mostly affect small oozoids which comprised 3% of sam-
16 ples (Henschke et al. 2021). Correspondingly at each station, hydrographic characteristics were
17 sampled with a SeaBird SBE 19+ Conductivity-Temperature-Depth (CTD) probe equipped with
18 a calibrated Chelsea Aqua-Tracker Mk2 fluorometer.

19
20 *S. thompsoni* individuals were sexed into oozoids or blastozooids, measured for the oral-atrial
21 body length (OAL) and their maturity stage identified (Foxton, 1966). Oozoids (stages 0 – 3) are
22 reproductively immature until the development and release of blastozooid buds (stage 4
23 onwards). Blastozooids begin 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
26 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 *S. thompsoni* (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 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 ($F_{1,31}$
42 = 6.08, $p = 0.02$). Blastozooids (15.55 ± 24.86 individuals (ind.) 1000 m^{-3}) and oozoids ($10.26 \pm$
43 14.24 ind. 1000 m^{-3}) were approximately 20-fold more abundant during the night than during the
44 day (blastozooid: 0.48 ± 0.85 ind. 1000 m^{-3} ; oozoid: 0.94 ± 1.19 ind. 1000 m^{-3}).

45

46 Blastozooids and oozoids both displayed pronounced diel vertical migration, with weighted
47 mean depths much deeper during the day (blastozooids: 449 m, oozoids: 465 m) than at night
48 (blastozooids: 87 m, oozoids: 115 m; Fig. 2). Blastozooids were absent above 300 m during the
49 day, whereas a small proportion (10%) of large, reproductive oozoids (77 – 89 cm) were present.

50

51 Juvenile females (10 - 25 mm; Table 2) made up the majority of the blastozooid population in
52 surface waters (0 – 100 m) at night (Fig. 3a). In deeper layers (300 – 600 m), juvenile females
53 were more dominant during the day, showing a similar size distribution to the night time surface
54 samples, whereas larger blastozooids became more dominant at night (Fig. 3c). At night
55 reproducing females and males were 20 to 40 times more abundant in deeper water (300 – 600
56 m; Fig. 3e; Table 2).

57

58 In general, the size distributions of oozoids were more evenly distributed in surface water (Fig.
59 3b), with peaks in juvenile and reproducing oozoids (Table 2). Reproductively immature
60 individuals (< 50 mm; Table 2) made up the largest proportion of oozoids during the day in deep
61 water (Fig. 3c), whereas the 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

66 **Discussion**

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-rich surface layers
75 (Nishikawa and Tsuda 2001, Pakhomov et al., 2011). While the whole population was
76 performing diel-vertical migration, this migration varied depending on *S. thompsoni* size and
77 stage. Blastozooids and oozoids were absent in the top 300 m during the day time, with the
78 exception of a small proportion of very large, reproducing oozoids. Residing in surface waters
79 during the day time may expose salps to visual predators, with midwater fish, seabirds and seals
80 suggested to be potential consumers (Pakhomov et al., 2002, Henschke et al. 2016). Midwater
81 fish are nocturnal feeders and generally prey on small salp individuals (Saunders et al., 2019).
82 Hence, the main potential predators for the 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 near-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 significant 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
95 oozoids were major contributors to the population's vertical migrations into the surface water.

96

97 Interestingly, the majority of blastozoid and oozoid size classes were at least 2 times more
98 abundant at night at 300-600 m, suggesting their daytime residence at much deeper layers.
99 Larger and mature blastozoids (25 - 32 and 44 - 52 mm) and oozoids (60 - 75 mm) were 10 –
100 40 times more abundant at night in deep water. This concurs with previous findings that embryo
101 (young oozoid) release may occur below the euphotic zone (Foxton, 1966, Casareto and Nemoto,
102 1986). Nevertheless, this phenomenon requires further investigation because the largest
103 blastozoids are likely all functional males and currently we do not know when the egg
104 fertilization in young blastozoids occurs. Previously, it has been proposed that chain release
105 mainly occurs near the surface (Foxton, 1966). Therefore, active migration of small to medium
106 blastozoids would be ecologically justified because they are the most actively growing
107 specimens that could be under heavy predation pressure. We did observe the smallest
108 blastozoids (≤ 10 mm) in deeper layers at nighttime, allowing us to hypothesize that chain
109 release may also occasionally occur below the euphotic zone, which corresponds with higher
110 proportions of larger reproductive oozoids displaying a deeper daytime residence. This however
111 requires confirmation because it could also be an artifact of sample contamination during trawl
112 deployment (Henschke et al., 2021).

113

114 The higher night time proportions of larger blastozoids and oozoids at depths 300 - 600 m, and
115 their weighted mean depth of ~ 450 m, implies that large size classes of *Salpa thompsoni* may be
116 migrating from even deeper layers. In this study they were found to 800 m during the day, albeit
117 in low abundances. During the current study, the deepest sampling events were rare (2 out of 47
118 trawls), with the majority of sampling (47 %) undertaken in the top 300 m. A more detailed
119 sampling program is required to explore the maximum depth distribution and residency of
120 various stages and sizes of *S. thompsoni*. However, depth-integrated night time salp abundances
121 were ~ 20 times greater than daytime abundances. While the deepest sampling depths in this
122 study could be misrepresented due to lower sample sizes, sampling effort at each depth was
123 similar between day and night further suggesting that the daytime residence of *S. thompsoni*
124 could be below 800 m. In this study, tows were targeting high backscattering signals, hence it is
125 possible that target tows missed layers with high salp densities because they may have been
126 acoustically invisible. At one station there were strong patches migrating at mid-day from ~ 200
127 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 may be dictated by the salp
137 size (Lüskow et al. 2020). This knowledge is critical, particularly in modelling salp contributions
138 to the vertical passive and active carbon fluxes.

139

140

141 **Acknowledgements**

142

143 We thank B. Quéguiner, the PI of the MOBYDICK project, for providing us the opportunity to
144 participate to this cruise, the chief scientist I. Obernosterer and the captain and crew of the R/V
145 *Marion Dufresne* for their enthusiasm and support aboard during the MOBYDICK–THEMISTO
146 cruise (<https://doi.org/10.17600/18000403>). This work was supported by the French
147 oceanographic fleet (“*Flotte océanographique française*”), the French ANR (“*Agence Nationale*
148 *de la Recherche*”, AAPG 2017 program, MOBYDICK Project number: ANR-17-CE01-0013),
149 and the French Research program of INSU-CNRS LEFE/CYBER (“*Les enveloppes fluides et*
150 *l’environnement*” – “*Cycles biogéochimiques, environnement et ressources*”). This research was
151 partially supported by the NSERC Discovery Grant RGPIN-2014-05107 held by EA Pakhomov.

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

Depth layer (m)	Day		Night	
	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	505	2
600-700	642	3	626	3
700-800	814	1	802	1

239

240

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

Blastozoid			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	25.25	102
3	26.06	80	3	34.36	203
4	31.34	5	4	52.18	244
5	36.73	338	4.5	65.91	106
6	22.63	333	5	80.68	55
			5.5	89.66	35

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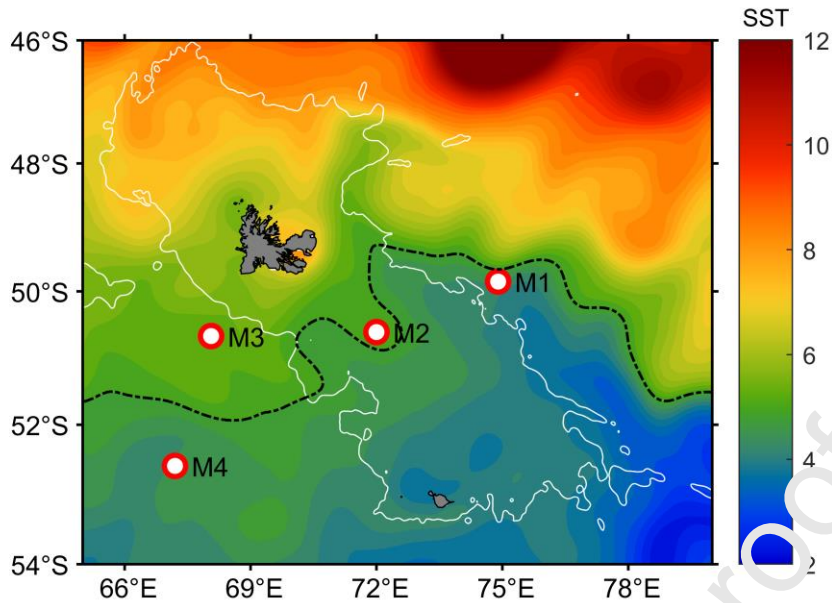
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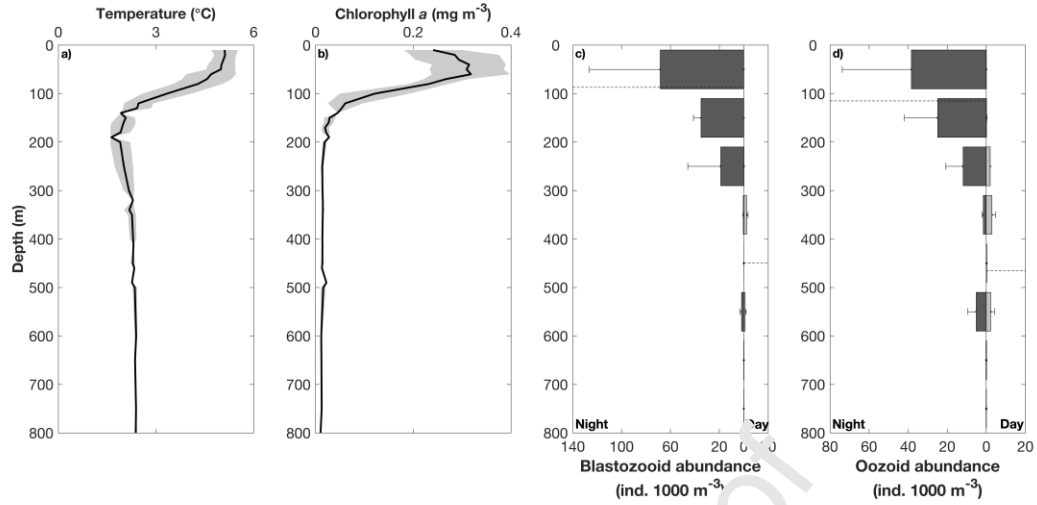
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252
253 Figure 1. Map of stations sampled during the MOBYDICK expedition, from 26 February to 19
254 March 2018 with average sea surface temperature (SST) overlaid. Dashed line represents the 5
255 degree isotherm. SST data were retrieved using the Copernicus platform
256 (<http://marine.copernicus.eu>). Data were produced by running the OSTIA system, a merged,
257 multi-sensor L4 Foundation SST product, with a spatial resolution of 0.05 degrees (Donlon et al.
258 2012). The continental slope (continuous white line, 1000 m isobath) and the Polar Front (dashed
259 black line, 5°C SST) are represented.

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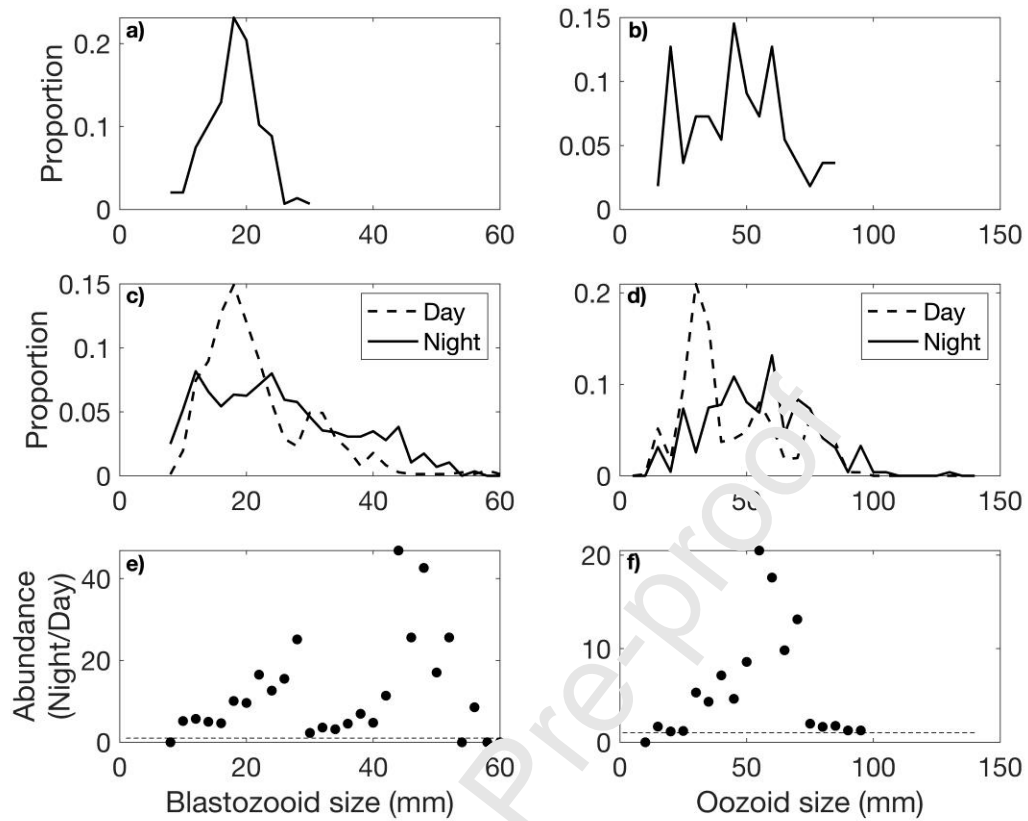
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266 Figure 2. Mean (\pm SD) temperature (a), chlorophyll *a* biomass (b) and mean (\pm SE) day/night267 vertical distribution of *Salpa thompsoni* blastozoids (c) and oozoids (d). Dashed lines in c-d

268 indicate weighted mean depth.

269



270

271

272 Figure 3. Proportional size distribution of *Salpa thompsoni* blastozoids (a, c) and
 273 oozoids (b, d) in the surface (0 – 100 m.; top row) and deep (300 – 600 m.; middle row)
 274 layer. Blastozoids and oozoids were only sampled during the night in surface water so
 275 there are no daytime values. Hence the Night/Day abundance ratio of blastozoids (e) and
 276 oozoids (f) by size bin is only available for the deep layer.

277 Supplementary Information

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

281

Site	Location (°S, °E)	Visit	Sampling date (DD/MM/YY)	Day/ Night	Sampling depth (m)	Visit	Sampling date (DD/MM/YY)	Day/ Night	Sampling depth (m)	Visit	Sampling date (DD/MM/YY)	Day/ Night	Sampling depth (m)
M1	49.85, 74.90	1	09/03/18	D	400								
				D	50								
				D	632								
				N	51								
				N	290								
				N	617								
M2	50.62, 72.00	1	26/02/18 – 27/02/18	D	NS	2	07/03/18	D	170	3	16/03/18 – 17/03/18	D	105
				D	210			D	70			D	340
				D	350			D	350			D	190
				N	340			N	317			N	65
				N	57			N	50			N	377
				N	158			N	175			N	30
				N	158			N	175			N	30
M3	50.68, 68.06	1	4/03/18*, 15/03/18	D	55*	2	18/03/18 – 19/03/18	D	814				
				D	460*			D	600				
				D	683			D	65				
				N	610			N	802				
				N	90			N	650				
				N	415			N	73				
M4	52.60, 67.20	1	01/03/18 – 02/03/18	D	93	2	14/03/18	D	85				
				D	575			D	610				
				D	425			D	410				
				N	400			N	600				

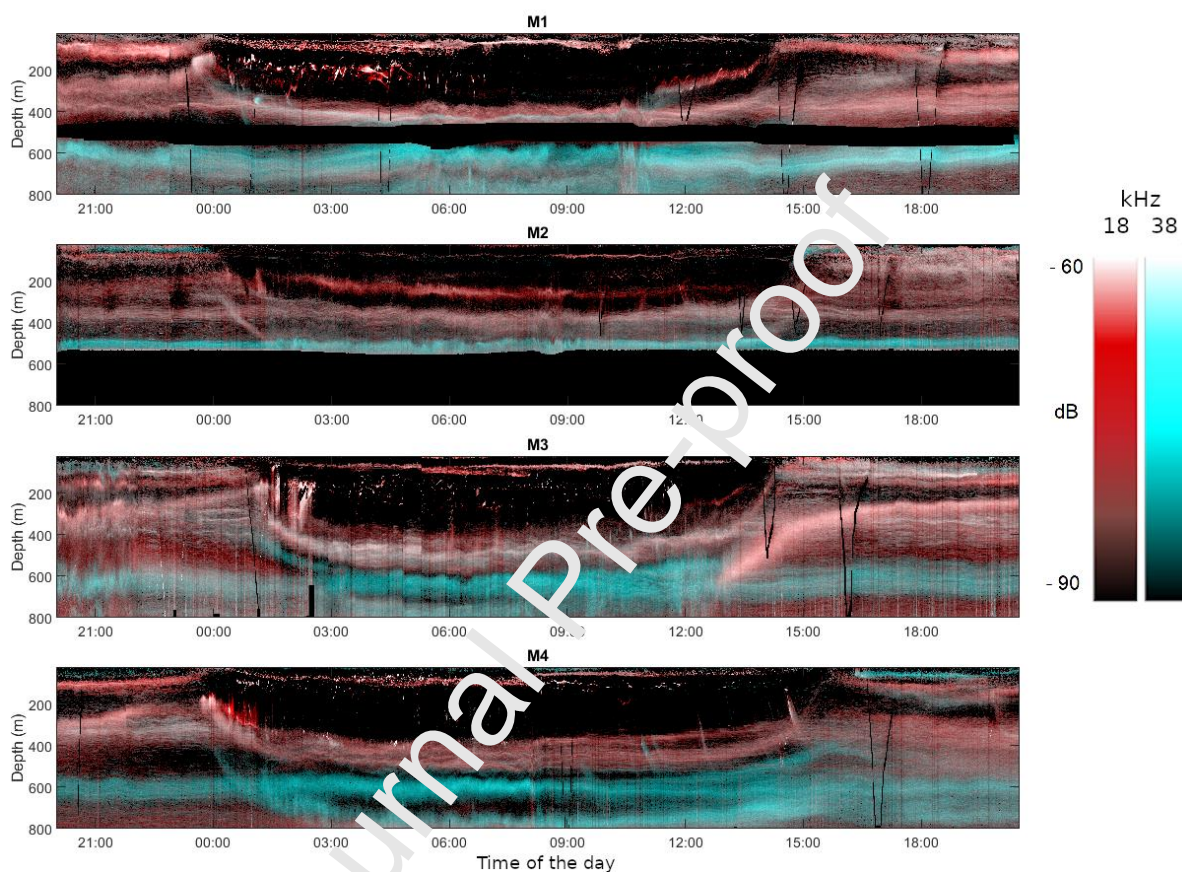
N 96
N 575

N 80
N 400

282 * 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
283 remaining day and night events occurred on 15/03/18.

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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.

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