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

Natasha Henschke\(^a,^*\), Yves Cherel\(^b\), Cédric Cotté\(^c\), Boris Espinasse\(^a,d\), Brian P.V. Hunt\(^a,d,e\), Evgeny A. Pakhomov\(^a,d,e\)

\(^a\) Department of Earth, Ocean and Atmospheric Sciences, University of British Columbia, Vancouver, British Columbia, Canada
\(^b\) Centre d’Études Biologiques de Chizé (CEBC), UMR 7372 CNRS-La Rochelle Université, 79360 Villiers-en-Bois, France
\(^c\) Sorbonne Université, CNRS, IRD, MNHN, Laboratoire d’Océanographie et du Climat: Expérimentations et Approches Numériques (LOCEAN-JPSL), Paris, France
\(^d\) Institute for the Oceans and Fisheries, University of British Columbia, Vancouver, British Columbia, Canada
\(^e\) Hakai Institute, PO Box 309, Heriot Bay, BC, Canada

**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 migrations, 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 nighttime weighted mean depth of ~100 m. Smaller blastozooids and oozoids were the strongest vertical migrants, 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.

1. 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 and 600 m during the daytime (e.g., Cazareto 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. Blastozooids 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 (Cazareto and Nemoto, 1986; Lancraft et al., 1989; Lancraft et al., 1991; 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).

\(^*\) Corresponding author.

E-mail address: nhenschke@eoas.ubc.ca (N. Henschke).

https://doi.org/10.1016/j.jmarsys.2021.103587

Received 31 December 2020; Received in revised form 25 May 2021; Accepted 28 May 2021

Available online 1 June 2021

0924-7963/© 2021 Published by Elsevier B.V.
Vertical migrators are increasingly important to biogeochemical cycling, particularly for species such as *Salpa 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 at the very end of the productive period.

2. Methods

*Salpa thompsoni* sampling was undertaken on the RV *Marion Dufresne II* at four stations near and on the Kerguelen Plateau during the “Marine Ecosystem Biodiversity and Dynamics of Carbon around Kerguelen: an integrated view” (MORBYDICK) expedition between February 26 and March 19, 2018 (Fig. 1). This voyage was a continuation of three previous programs in the area, with stations chosen to coincide with previously sampled areas. For more details on the sampling design and population demographics of *S. thompsoni* from this study see Henschke et al. (2021). The Kerguelen Plateau region has the largest seasonal phytoplankton blooms of any Southern Ocean island systems (Blain et al., 2007) and is an important feeding ground for fish populations and top predators (Guinet et al., 1996; Cherel et al., 2005). At each station, daytime (0700–1400) and nighttime (0000–0200) trawls were conducted using the Mesopelagos trawl (Meillat, 2012) in surface (50–100 m), middle (200–650 m) and deep (300–800 m) layers (Table 1; Table S1). Due to the large mesh size in the trawl, these samples may consistently underestimate individuals smaller than 25 mm, however, as small blastozooids generally occur in chains the undersampling is likely to mostly affect small oozoids which comprised 3% of samples (Henschke et al., 2021). Correspondingly, at each station, hydrographic characteristics were sampled with a SeaBird SBE 19+ Conductivity- Temperature-Depth (CTD) probe equipped with a calibrated Chelsea Aqua-Tracker Mk3 fluorometer.

*S. thompsoni* individuals were sexed into oozoids or blastozooids, measured for the oral-atrial body length (OAL) and their maturity stage identified (Foxton, 1966). Oozoids (stages 0–3) are reproductively immature until the development and release of blastozooid buds (stage 4 onwards). Blastozooids begin as reproductively immature females (stage 0–3). Once reproductive, they release an oozoid embryo at stage 4, and then develop testis and function as a 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 dynamics see Henschke et al. (2021).

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

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

where \(a_i\) is the abundance of *S. thompsoni* (ind. m\(^{-3}\)) and \(d_i\) is the midpoint of the depth stratum in each sampling location i.

To determine size-specific migration, blastozooids and oozoids were binned into 1 and 5 mm size intervals respectively before calculating the night/day abundance ratios in deep (300–600 m) layers. A ratio greater than 1 indicates higher proportions of that size class occurring at that respective depth (surface or deep) at nighttime. This ratio was not calculated at other depths as it requires both day and night size distributions; daytime distributions were mostly absent in surface water (0–100 m).

3. Results

*Salpa thompsoni* were sampled down to depths of 814 m during the day and 802 m at night. Depth integrated nighttime abundance was significantly greater than daytime abundances (\(F_{1,31} = 6.08, p = 0.02\)). Blastozooids (15.55 ± 24.86 individuals (ind.) 1000 m\(^{-3}\)) and oozoids (10.26 ± 14.24 ind. 1000 m\(^{-3}\)) were approximately 20-fold more abundant during the night than during the day (blastozooid: 0.48 ± 0.85 ind. 1000 m\(^{-3}\); oozoid: 0.94 ± 1.19 ind. 1000 m\(^{-3}\)).

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

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

In general, the size distributions of oozoids were more evenly distributed in surface water (Fig. 3b), with peaks in juvenile and
reproducing oozoids (Table 2). Reproductively immature individuals (< 50 mm; Table 2) made up the largest proportion of oozoids during the day in deep water (Fig. 3c), whereas the nighttime distribution was characterized by higher proportions of reproducing individuals (50–75 mm). Reproducing individuals also made up the largest change in density; 10–20 times more abundant at night than during the day in deep water (Fig. 3f).

4. Discussion

Salpa thompsoni populations on the Kerguelen Plateau were undergoing diel vertical migration from a daytime weighted mean depth of ~450 m to a nighttime weighted mean depth of ~100 m. This pattern had been well documented during previous studies and salps often have been observed visually near the surface at night (Cazareto and Nemoto, 1986; Lancraft et al., 1989; Krakatitsa et al., 1993; Perissinotto and Pakhomov, 1998; Conroy et al., 2020). In our study, the highest nighttime abundances indeed occurred in the top 300 m during the daytime, with the exception of a small proportion of very large, reproducing oozoids. Residing in surface waters during the daytime may expose salps to visual predators, with midwater fish, seabirds and seals suggested to be potential consumers (Pakhomov et al., 2002; Henschke et al., 2016). Midwater fish are nocturnal feeders and generally prey on small salp individuals (Saunders et al., 2019). Hence, the main potential predators for the large oozoids would be seabirds and seals; however, observations of penguin or seal predation are rare (Thiebot and McInnes, 2019). If the large oozoids in this study avoided the near-surface layers (0–30 m), they may circumvent daytime predation from seabirds but not diving penguins or seals. Oozoids of this size (80–90 mm) would be producing up to 2 chains of 250 identical blastozooid buds (Daponte et al., 2001), which would require a significant amount of energy (Henschke et al., 2018). Hence, it is plausible that reproducing oozoids are choosing to remain in the food-rich surface layers during the daytime to maximize their energy intake for reproduction.

Fig. 2. Mean (±SD) temperature (a), chlorophyll a biomass (b), and mean (±SE) day/night vertical distribution of Salpa thompsoni blastozooids (c) and oozoids (d). Dashed lines in c-d indicate weighted mean depth.

Table 2

<table>
<thead>
<tr>
<th>Blastozooid</th>
<th>Mean size (mm)</th>
<th>n</th>
<th>Oozoid</th>
<th>Mean size (mm)</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>13.21</td>
<td>509</td>
<td>0</td>
<td>5.40</td>
<td>7</td>
</tr>
<tr>
<td>1</td>
<td>17.51</td>
<td>291</td>
<td>1</td>
<td>19.46</td>
<td>16</td>
</tr>
<tr>
<td>2</td>
<td>22.65</td>
<td>539</td>
<td>2</td>
<td>25.25</td>
<td>102</td>
</tr>
<tr>
<td>3</td>
<td>26.66</td>
<td>80</td>
<td>3</td>
<td>34.36</td>
<td>203</td>
</tr>
<tr>
<td>4</td>
<td>31.34</td>
<td>5</td>
<td>4</td>
<td>52.18</td>
<td>244</td>
</tr>
<tr>
<td>5</td>
<td>36.73</td>
<td>38</td>
<td>4.5</td>
<td>65.91</td>
<td>106</td>
</tr>
<tr>
<td>6</td>
<td>22.63</td>
<td>333</td>
<td>5</td>
<td>80.68</td>
<td>55</td>
</tr>
<tr>
<td>5.5</td>
<td>36.48</td>
<td>333</td>
<td>5.5</td>
<td>89.66</td>
<td>35</td>
</tr>
</tbody>
</table>

Interestingly, the majority of blastozooid and oozoid size classes were at least 2 times more abundant at night than during the day in deep water. The blastozooids were the predominant size group and constituted the majority of the population. This is consistent with previous studies that have observed salps to be more abundant near the surface at night (Cazareto and Nemoto, 1986; Perissinotto and Pakhomov, 1998; Lüskow et al., 2020). In our study, the highest nighttime abundances indeed occurred in the top 300 m during the daytime, with the exception of a small proportion of very large, reproducing oozoids. Residing in surface waters during the daytime may expose salps to visual predators, with midwater fish, seabirds and seals suggested to be potential consumers (Pakhomov et al., 2002; Henschke et al., 2016). Midwater fish are nocturnal feeders and generally prey on small salp individuals (Saunders et al., 2019). Hence, the main potential predators for the large oozoids would be seabirds and seals; however, observations of penguin or seal predation are rare (Thiebot and McInnes, 2019). If the large oozoids in this study avoided the near-surface layers (0–30 m), they may circumvent daytime predation from seabirds but not diving penguins or seals. Oozoids of this size (80–90 mm) would be producing up to 2 chains of 250 identical blastozooid buds (Daponte et al., 2001), which would require a significant amount of energy (Henschke et al., 2018). Hence, it is plausible that reproducing oozoids are choosing to remain in the food-rich surface layers during the daytime to maximize their energy intake for reproduction.

Juvenile blastozooids (10–25 mm) migrated into surface waters during the night from daytime depths between 300 and 600 m. This was observed in the Pacific Sector of the subantarctic region (Lüskow et al., 2020). Correspondingly, juvenile oozoids (20–60 mm) also migrated into surface water at nighttime. 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.
predation pressure. We did observe the smallest blastozooids (≤ 10 mm) in deeper layers at nighttime, allowing us to hypothesize that chain release may also occasionally occur below the euphotic zone, which corresponds with higher proportions of larger reproductive oozoids displaying a deeper daytime residence. This however requires confirmation because it could also be an artifact of sample contamination during trawl deployment (Henschke et al., 2021).

The higher nighttime proportions of larger 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 layers. 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 majority of sampling (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 nighttime 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 found to migrate upward when solar radiation is at its strongest (Nishikawa and Tsuda, 2001). More detailed analysis on the ability to detect S. thompsoni in acoustic backscattering layers is needed to elucidate this theory.

In summary, smaller blastozooids and oozoids were the strongest vertical migrators, while their larger counterparts may have either a longer, or/and deeper migration cycle; but this is still poorly understood. Strong vertical migrations of the smallest blastozooids and oozoids could imply high predation pressure on these groups and thus their importance to higher trophic levels. It has been postulated that the intensity of salp vertical migrations may be dictated by the salp size (Lüskow et al., 2020). This knowledge is critical, particularly in modelling salp contributions to the vertical passive and active carbon fluxes.

Declaration of Competing Interest

None.

Acknowledgements

We thank B. Quéguiner, the PI of the MOBYDICK project, for providing us the opportunity to participate to this cruise, the chief scientist I. Obernosterer and the captain and crew of the R/V Marion Dufresne for their enthusiasm and support aboard during the MOBYDICK–THEMISTO cruise (https://doi.org/10.17600/18009043). This work was supported by the French oceanographic fleet (“Flotte oceanographique française”), the French ANR (“Agence Nationale de la Recherche”, AAPG 2017 program, MOBYDICK Project number: ANR-17-CE01-0013), and the French Research program of INSU-CNRS LEFE/CYBER (“Les enveloppes fluides et l’environnement” – “Cycles biogéochimiques, environnement et ressources”). This research was partially supported by the NSERC Discovery Grant RGPIN-2014-05107 held by EA Pakhomov.
Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jmarsys.2021.103587.

References


