



## 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 nighttime 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.

### 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; 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).

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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 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” (MOBYDICK) 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 (1900–0200) 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

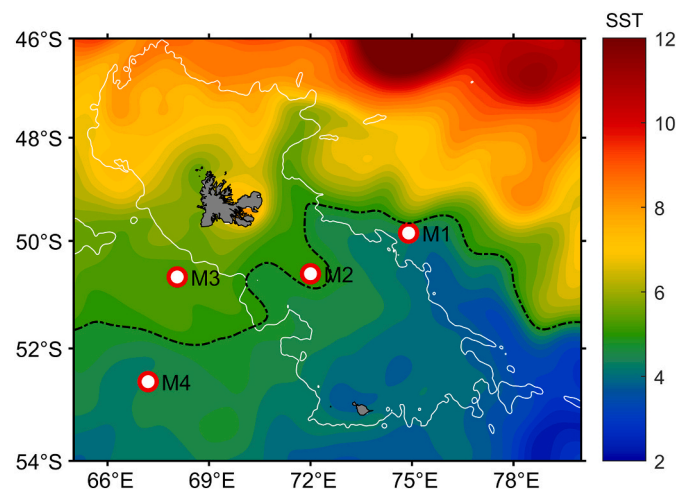


Fig. 1. Map of stations sampled during the MOBYDICK expedition, from 26 February to 19 March 2018 with average sea surface temperature (SST) overlaid. Dashed line represents the 5 degree isotherm. SST data were retrieved using the Copernicus platform (<http://marine.copernicus.eu>). Data were produced 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.

Table 1

Count of trawls (n) undertaken in each depth layer. For more detail on station 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	588	2
600–700	642	3	626	3
700–800	814	1	802	1

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).

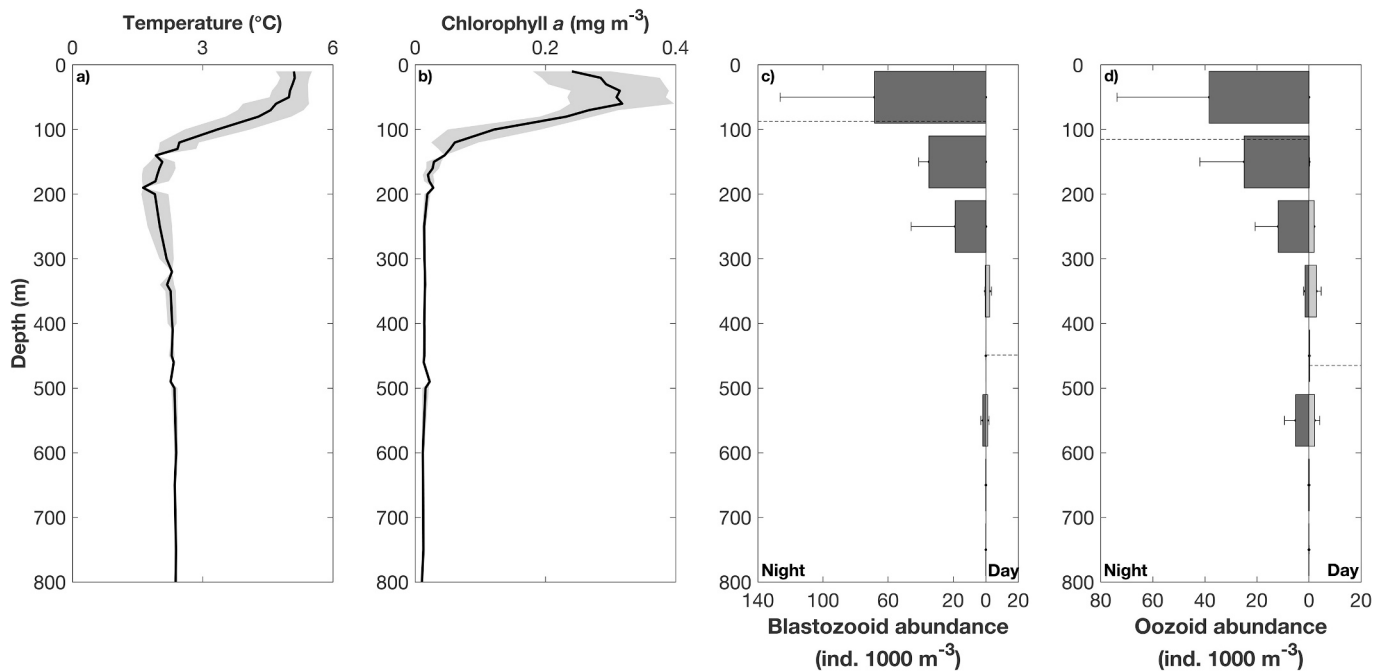
## 3. Results

*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 ( $15.55 \pm 24.86$  individuals (ind.)  $1000 m^{-3}$ ) and oozoids ( $10.26 \pm 14.24$  ind.  $1000 m^{-3}$ ) were approximately 20-fold more abundant during the night than during the day (blastozooid:  $0.48 \pm 0.85$  ind.  $1000 m^{-3}$ ; oozoid:  $0.94 \pm 1.19$  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



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

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

Blastozooid			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

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**

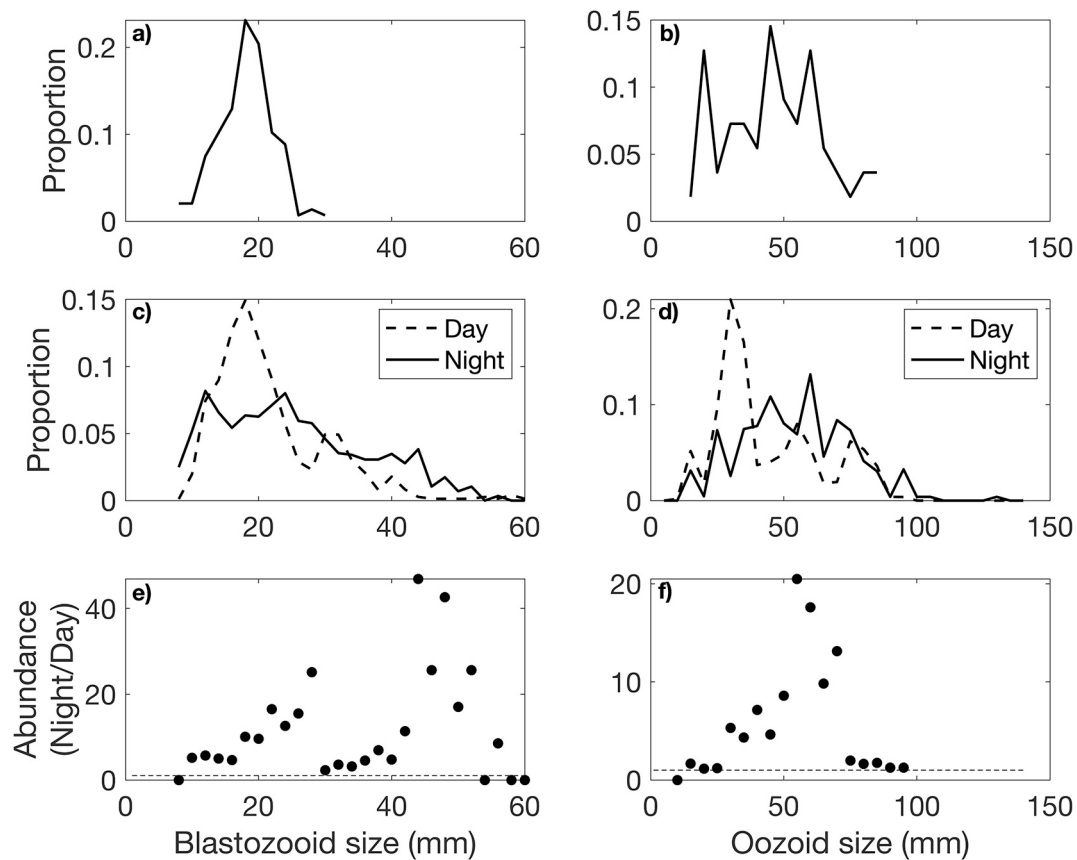
*Salpa thompsoni* populations on the Kerguelen Plateau were undergoing diel vertical migration from a daytime weighted mean depth of ~450 m to a nighttime weighted mean depth of ~100 m. This pattern had been well documented during previous studies and salps often have been observed visually near the surface at night (Cazareto and Nemoto, 1986; Lanrcraft 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 100 m, which corresponded with the chlorophyll *a* maximum. This suggests that, like in other parts of the Southern Ocean, the *S. thompsoni* population was migrating to take advantage of the food-rich surface layers (Nishikawa and Tsuda, 2001; Pakhomov et al., 2011). While the whole population was performing diel-vertical migration, this migration varied depending on *S. thompsoni* size and stage. Blastozooids and oozoids were absent 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 (Luskow 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.

Interestingly, the majority of blastozooid and oozoid size classes 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; Cazareto 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



**Fig. 3.** Proportional size distribution of *Salpa thompsoni* blastozooids (a, c) and oozoids (b, d) in the surface (0–100 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 is only available for the deep layer. Dashed line represents Night/Day abundance ratio of 1.

predation pressure. We did observe the smallest blastozooids ( $\leq 10$  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  $\sim 450$  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  $\sim 20$  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  $\sim 200$  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 (Luskow 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.

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## Appendix A. Supplementary data

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

## References

- Blain, S., Quéguiner, B., Armand, L.K., Belviso, S., Bomble, B., Bopp, L., et al., 2007. Impacts of natural iron fertilisation on the Southern Ocean. *Nature*. 446, 1070–1074.
- Bruland, K.W., Silver, M.W., 1981. Sinking rates of fecal pellets from gelatinous zooplankton (Salps, Pteropods, Doliolids). *Mar Biol.* 63, 295–300.
- Cazareto, B.E., Nemoto, T., 1986. Salps of the Southern Ocean (Australian sector) during the 1982–84 summer, with special reference to the species *Salpa thompsoni*, Foxton 1961. *Mem. Natl. Inst. Polar Res.* 40, 221–239.
- Cherel, Y., Bost, C.-A., Guinet, C., Weimerskirch, H., Feeding habits of seabirds and marine mammals of the Kerguelen Archipelago. In: Palomares MLDea, editor. *Modeling Antarctic Marine Ecosystems*. 13(7): Fisheries Center Research Reports; 2005. p. 31–6.
- Conroy, J.A., Steinberg, D.K., Thibodeau, P.S., Schofield, O., 2020. Zooplankton diel vertical migration during Antarctic summer. *Deep-Sea Res.* 1 162, 103324.
- Daponte, M.C., Capitanio, F.L., Esnal, G.B., 2001. A mechanism for swarming in the tunicate *Salpa thompsoni* (Foxton, 1961). *Antarct. Sci.* 13, 240–245.
- Foxton, P., 1966. The distribution and life-history of *Salpa thompsoni* Foxton with observations on a related species, *Salpa gerlachei* Foxton. *Discov. Rep.* 34, 1–116.
- Guinet, C., Cherel, Y., Ridoux, V., Jouventin, P., 1996. Consumption of marine resources by seabirds and seals in Crozet and Kerguelen waters: changes in relation to consumer biomass 1962–85. *Antarct. Sci.* 8, 23–30.
- Henschke, N., Pakhomov, E.A., 2018. Latitudinal variations in *Salpa thompsoni* reproductive fitness. *Limnol. Oceanogr.* 64, 575–584.
- Henschke, N., Everett, J.D., Richardson, A.J., Suthers, I.M., 2016. Rethinking the role of salps in the ocean. *Trends Ecol. Evol.* 31, 720–733.
- Henschke, N., Pakhomov, E.A., Groeneveld, J., Meyer, B., 2018. Modelling the life cycle of *Salpa thompsoni*. *Ecol. Model.* 387, 17–26. <https://doi.org/10.1016/j.ecolmodel.2018.08.017>.
- Henschke, N., Blain, S., Cherel, Y., Cotté, C., Espinasse, B., Hunt, B.P.V., Pakhomov, E.A., 2021. Population demographics and growth rate of *Salpa thompsoni* on the Kerguelen Plateau. *J. Mar. Syst.* 214.
- Heron, A.C., 1972. Population ecology of a colonizing species - pelagic tunicate *Thalia democratica*. 2. Population growth-rate. *Oecologia* 10, 294–312.
- Krakatitsa, V.V., Karpenko, G.P., Pakhomov, E.A., 1993. Distribution peculiarities of zooplankton depending on temperature stratification of the 1-metre surface water layer in the Cooperation Sea. In: Voronina, N.M. (Ed.), *Pelagic Ecosystems of the Southern Ocean*. Nauka Press, Moscow, pp. 151–157 (in Russian).
- Lancraft, T.M., Torres, J.J., Hopkins, T.L., 1989. Micronekton and macrozooplankton in the open waters near Antarctic ice edge zones (AMERIEZ 1983 and 1986). *Polar Biol.* 9, 225–233.
- Lancraft, T.M., Hopkins, T.L., Torres, J.J., Donnelly, J., 1991. Oceanic micronektonic/macrozooplanktonic community structure and feeding in the ice covered Antarctic waters during the winter (AMERIEZ 1988). *Polar Biol.* 11, 157–167.
- Liiskow, F., Pakhomov, E.A., Stukel, M.R., Décima, M., 2020. Biology of *Salpa thompsoni* at the Chatham rise, New Zealand: demography, growth, and diel vertical migration. *Mar. Biol.* 167, 175. <https://doi.org/10.1007/s00227-020-03775-x>.
- Manno, C., Stowasser, G., Enderlein, P., Fielding, S., Tarling, G.A., 2015. The contribution of zooplankton faecal pellets to deep-carbon transport in the Scotia Sea (Southern Ocean). *Biogeosciences*. 12, 1955–1965.
- Meillat, M., 2012. Essais du Chalut Mesopelagos Pour le Programme MYCTO 3D-MAP de l'IRD, a Bord du Marion Dufresne (du 10 au 21 aout 2012).
- Nishikawa, J., Tsuda, A., 2001. Diel vertical migration of the tunicate *Salpa thompsoni* in the Southern Ocean during summer. *Polar Biol.* 24, 299–302.
- Pakhomov, E.A., 1993. Vertical distribution and diel migrations of Antarctic macroplankton. In: Voronina, N.M. (Ed.), *Pelagic Ecosystems of the Southern Ocean*. Nauka Press, Moscow, pp. 146–150 (in Russian).
- Pakhomov, E.A., 1994. Diel vertical migrations of Antarctic macroplankton. Salpidae, Ctenophora, Coelenterata, Chaetognatha, Polychaeta, Pteropoda. *Oceanology* 33, 510–511.
- Pakhomov, E.A., Froneman, P.W., Perissinotto, R., 2002. Salp/krill interactions in the Southern Ocean: spatial segregation and implications for the carbon flux. *Deep-Sea Res.* II 49, 1881–1907.
- Pakhomov, E.A., Hall, J., Williams, M., Hunt, B.P.V., Stevens, C., 2011. Biology of *Salpa thompsoni* in waters adjacent to the Ross Sea, Southern Ocean during austral summer 2008. *Polar Biol.* 34, 257–271.
- Parker, M.L., Fraser, W.R., Ashford, J., Patarnello, T., Zane, L., Torres, J.J., 2015. Assemblages of micronektonic fishes and invertebrates in a gradient of regional warming along the Western Antarctic peninsula. *J. Mar. Syst.* 152, 18–41.
- Perissinotto, R., Pakhomov, E.A., 1998. The trophic role of the tunicate *Salpa thompsoni* in the Antarctic marine ecosystem. *J. Mar. Syst.* 17, 361–374.
- Saunders, R.A., Hill, S.L., Tarling, G.A., Murphy, E.J., 2019. Mictophid fish (family Myctophidae) are central consumers in the food web of the Scotia Sea (Southern Ocean). *Front. Mar. Sci.* 6, 530. <https://doi.org/10.3389/fmars.2019.00530>.
- Thiebot, J.-B., McInnes, J., 2019. Why do marine endotherms eat gelatinous prey? *ICES J. Mar. Sci.* <https://doi.org/10.1093/icesjms/fsz208>.