

## RESEARCH ARTICLE

# Summertime tintinnids in surface water of the Weddell and Cosmonaut seas: community structure and relationships with different water masses

Jingyuan Li<sup>1,2,3,4</sup>, Haibo Li<sup>1,2,3</sup>, Chaofeng Wang<sup>1,2,3</sup>, Yuan Zhao<sup>1,2,3</sup>, Li Zhao<sup>1,2,3</sup>, Yi Dong<sup>1,2,3</sup> & Wuchang Zhang<sup>1,2,3</sup>

<sup>1</sup>CAS Key Laboratory of Marine Ecology and Environmental Sciences, Institute of Oceanology, Chinese Academy of Sciences, Qingdao, China; <sup>2</sup>Laboratory for Marine Ecology and Environmental Science, Qingdao National Laboratory for Marine Science and Technology, Qingdao, China; <sup>3</sup>Center for Ocean Mega-Science, Chinese Academy of Sciences, Qingdao, China; <sup>4</sup>University of Chinese Academy of Sciences, Beijing, China

## Abstract

Tintinnids (Ciliophora) are important microzooplankton grazers. In the Southern Ocean, they are found in the Antarctic Zone, Polar Front and Subantarctic Zone. The Antarctic Zone encompasses large gyres (Weddell Gyre and Ross Gyre) and the Antarctic Slope Current around the continent. The influence of these water masses on tintinnid communities has not been studied. This study investigated the tintinnid community structure in the Weddell and Cosmonaut seas in the summer of 2022. In the Weddell Gyre, tintinnid abundance was significantly lower in the interior than at the fronts. The dominant species differed between the east and west fronts: the proportion of *Codonellopsis gaussi* was high at the west front, whilst *Laackmanniella naviculaefera*, *Salpingella* sp. and *Salpingella faurei* showed high abundances at the east front. Tintinnid communities varied from inshore to offshore of the Cosmonaut Sea, possibly because of the influence from the Antarctic Slope Current and Antarctic Circumpolar Current. The Antarctic Slope Current was characterized by the occurrence of *Cymatocylis drygalskii*, whilst the Antarctic Circumpolar Current was characterized by *Codonellopsis glacialis*, *Cymatocylis convallaria* and *Cy. calyciformis*. We proposed that *Cy. drygalskii* can be used as an indicator of the Antarctic Slope Current. Moreover, we classify polymorphic *C. gaussi* into three types, in accordance with their loricae, and report their distribution characteristics in water masses. Our results contribute to a better understanding of tintinnid horizontal distribution in different parts of the Weddell Gyre and water masses and serve as a baseline for future studies of pelagic community responses to climate change in the Southern Ocean.

## Keywords

Antarctica; microzooplankton; ciliate; biogeographic distribution; indicator; sea currents

## Correspondence

Wuchang Zhang, CAS Key Laboratory of Marine Ecology and Environmental Sciences, Institute of Oceanology, Chinese Academy of Sciences, Qingdao 266071, China. E-mail: wuchangzhang@qdio.ac.cn

## Abbreviations

ACC zone: Antarctic Circumpolar Current zone  
ASC zone: Antarctic Slope Current zone  
OF: occurrence frequency

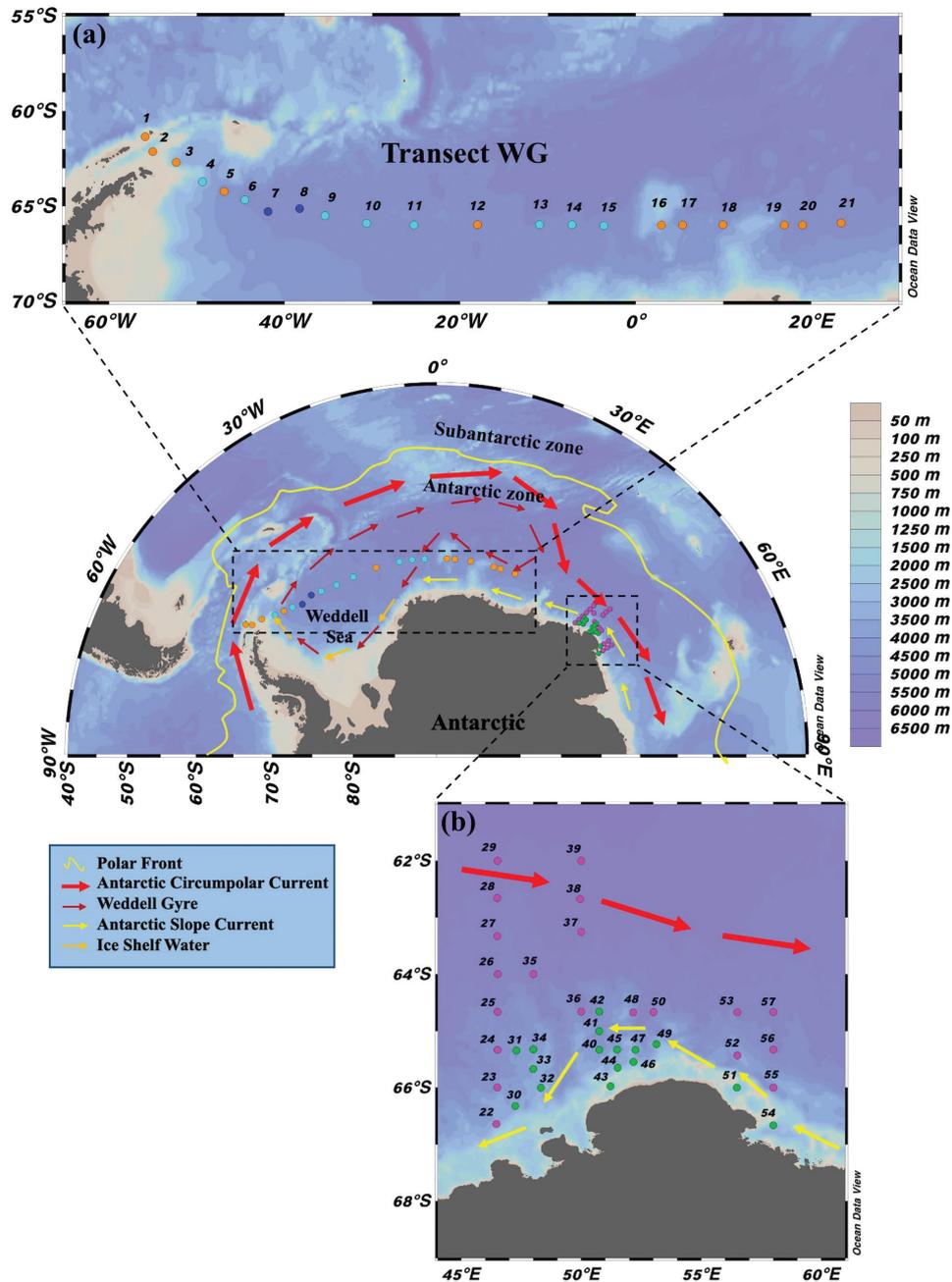
To access the supplementary material, please visit the article landing page

## Introduction

The Southern Ocean connects all the global ocean basins and has a key role in ocean circulation (Vernet et al. 2019). Two important boundary circulations in the Southern Ocean are the Antarctic Circumpolar Current in the north and the Antarctic Slope Current, which is in the south, close to the Antarctic continent (Fig. 1; Thoma et al. 2005; Thompson et al. 2018). The Antarctic Circumpolar Current divides the Southern Ocean into the Subantarctic Zone in the north and the Antarctic Zone in the south. The Antarctic Zone encompasses the

Weddell Gyre and Ross Gyre, which are major components of the Southern Ocean current system (Smith et al. 2007; Meredith et al. 2014). These currents play important roles in the heat transport and energy flow in the Southern Ocean and have an important impact on the distribution and survival of organisms.

Microzooplankton are an important part of the ecosystem in the Southern Ocean (Garrison 1991). They are primary consumers of small phytoplankton as well as important food sources for metazoans and fish larvae (Friedenberg et al. 2012; Rollwagen-Bollens et al. 2022). As microzooplankton with a cell size ranging



**Fig. 1** Sampling stations in the Weddell Sea and the Cosmonaut Sea. The sea currents are drawn from Thoma et al. (2005) and Hodgson et al. (2014). (a) Transect WG was comprised of stations 1–21, which crossed the Weddell Gyre. The colours of the dots representing the stations reflect the cluster analysis shown in Fig. 2. (b) Stations 22–57 sampled the Cosmonaut Sea. The colours of the dots reflect the cluster analysis in Fig. 3.

10–200  $\mu\text{m}$ , tintinnid ciliates are top grazers in the microbial food web. The diversity characteristics of tintinnids have been well investigated worldwide based on their species-specific lorica. Owing to their environmental sensitivity, tintinnids are valuable indicators of water masses in many sea regions, such as the coastal Ionian Sea (Sitran et al. 2007), Pacific and Atlantic oceans (Fonda Umani et al. 2011), north-eastern Mediterranean Sea (Polat

et al. 2019), Pacific Ocean (Li et al. 2021) and Arctic Ocean (Wang, Wang et al. 2022; Wang et al. 2023).

In the Southern Ocean, Dolan et al. (2012) divided tintinnid species into two groups: endemic species that occur in waters south of 40°S (Subantarctic and Antarctic) and widespread species recorded on both sides of 40°S. Antarctic large-scale biogeographic models further divide waters south of 50°S into Antarctic and Subantarctic

zones, with the Polar Front as the boundary between them (Thompson & Alder 2005). Liang et al. (2020) divided tintinnid communities into those that are found—from north to south—in the Antarctic Zone, Polar Front and Subantarctic Zone. The Antarctic Zone includes part of the Antarctic Circumpolar Current south of the Polar Front, the Weddell and Ross gyres and the Antarctic Slope Current. Tintinnid distributions within different water masses have been reported for the Antarctic Circumpolar Current of Prydz Bay (Liang et al. 2018), Cosmonaut and Cooperation seas (Li et al. 2022) and Amundsen and Ross seas (Wang, Xu et al. 2022). The characteristics of tintinnid communities in the Weddell Gyre and Antarctic Slope Current have not yet been reported.

Most tintinnid species have a morphologically unique lorica, which is an important basis for the traditional species taxonomy. However, some species may show polymorphism in lorica, a phenomenon that cannot be ignored in both the Arctic and Antarctic zones (Dolan et al. 2012). Recently, culture experiments on individuals of *Helicostomella* species and DNA experiments on individuals of *Leptotintinnus nordqvisti* have confirmed the polymorphism of tintinnid species (Santoferrara et al. 2015; Hu et al. 2022). Genetic studies (e.g., Kim et al. 2013) have confirmed the existence of polymorphism, but the distribution of different morphs is still not properly understood. Polymorphism in *Codonellopsis gaussi* has been recorded in the tintinnid survey in Antarctica, but the abundance distribution of *C. gaussi* in different parts of the Southern Ocean has not been specifically studied.

In the present study, we hypothesized that the tintinnid community differs in different water masses of the Weddell and Cosmonaut seas. By investigating tintinnid communities in surface waters along a west–east transect across the Weddell Gyre and a nearshore area in the Cosmonaut Sea, we aimed to uncover: (1) the distribution characteristics of tintinnid abundance and species composition in the Weddell Gyre, Antarctic Slope Current and Antarctic Circumpolar Current; (2) potential indicator functions of tintinnids for different water masses; and (3) the distribution of polymorphic *C. gaussi* individuals in the Weddell and Cosmonaut seas. Our research has important implications for the biogeography and response of microzooplankton to the rapid Antarctic warming process.

## Materials and methods

### Study area and sample collection

Tintinnid samples were collected during the 38th Chinese National Antarctic Research Expedition aboard the RV *Xuelong*. Transect WG, crossing the Weddell Gyre (stations 1–21), and the stations in the Cosmonaut Sea (stations

22–57) were sampled from 9 January to 11 March 2022 (Fig. 1, Supplementary Table S1).

At each station, 80 L of seawater was collected at a depth of 5 m using an onboard continuous underway sampling system and filtered through a 10- $\mu$ m aperture mesh net. Samples of stations 1–21 were taken when the ship was cruising in the Weddell Sea. Stations 22–57 were grid stations where samples were taken when the ship stopped for the investigation. Concentrated samples (approximately 100 ml) were fixed with Lugol's solution (1% final concentration). All samples were stored in dark, cool conditions until analysis. Temperature and salinity were obtained by the SBE911 conductivity–temperature–depth unit.

### Sample analysis and species identification

In the laboratory, a 5-ml subsample (or a larger volume if tintinnids were scarce) of each original sample was settled in an Utermöhl counting chamber (Utermöhl 1958) for at least 24 hours and then examined with an Olympus IX 73 inverted microscope at 100 $\times$  or 400 $\times$  magnification. We included empty tintinnid loricae in cell counts because mechanical and chemical disturbance during collection and fixation can detach tintinnid protoplasts from the lorica. Tintinnid species were identified using published studies, and *C. gaussi* was grouped into three types in accordance with the polymorphism described in the literature (Alder 1995; Dolan et al. 2012; Dolan et al. 2022; Wang, Xu et al. 2022).

### Data processing

Tintinnid abundance ( $A$ , ind/L) at each station was calculated using the counting data with the following equation:

$$A = \frac{N \times V_{\text{sample}}}{V_{\text{subsample}} \times V_{\text{seawater}}},$$

where  $N$  was the individual number of each species in the subsample,  $V_{\text{subsample}}$  was the volume (5 ml) of subsample,  $V_{\text{sample}}$  was the volume (approximately 100 ml) of each original sample and  $V_{\text{seawater}}$  was the volume (80 L) of filtered seawater.

Cluster analysis of the stations was conducted using the group-average linkage based on the Bray-Curtis similarity matrix of temperature and salinity. Figures were drawn using the software Ocean Data View, Prism 9 and PRIMER 5.

## Results

### Hydrography and water masses

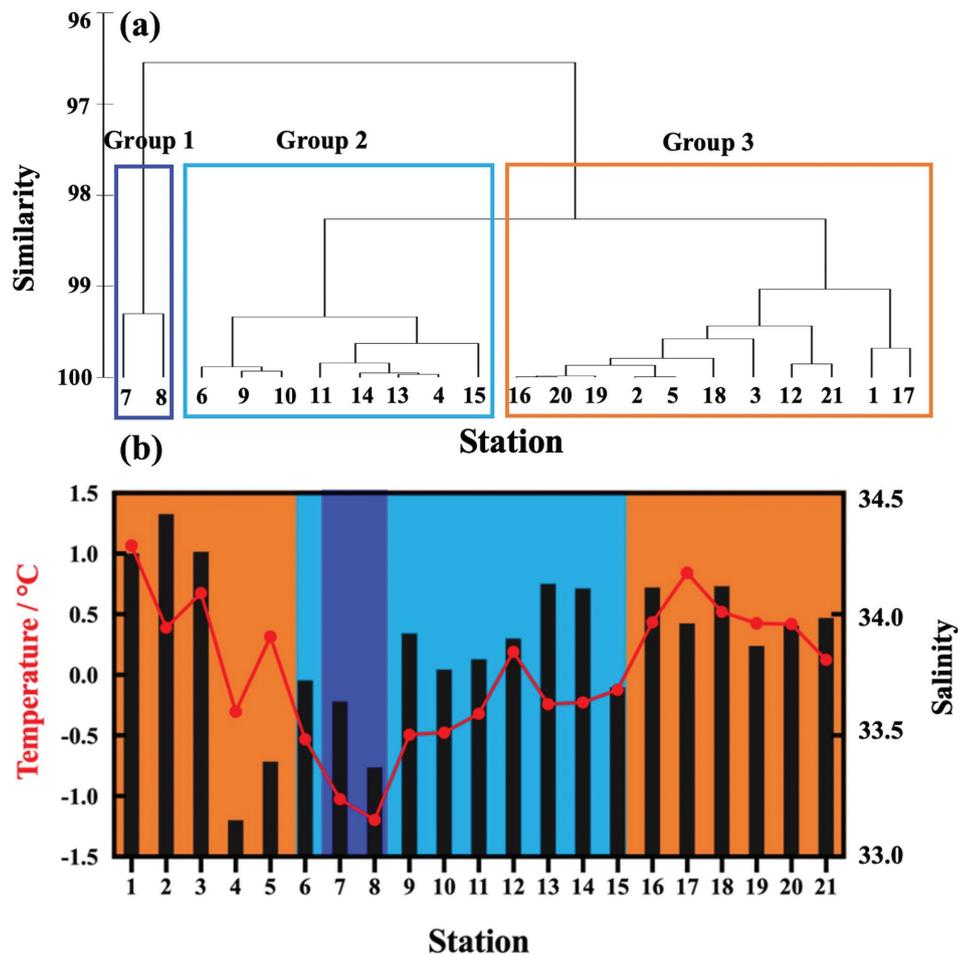
The temperature and salinity of Transect WG and the Cosmonaut Sea showed obvious variations (Figs. 2, 3).

The water mass structures of the Weddell and Cosmonaut seas were divided through cluster analysis of environmental factors. Stations in Transect WG were divided into three groups (Figs. 1a, 2): stations 7 and 8 comprised group 1, in the centre of the Weddell Gyre; group 2 (stations 6 and 9–15) included the other stations within the Weddell Gyre; group 3 stations (stations 1–5 and 16–21) were located at both ends of the transect, outside the Weddell Gyre. The temperature of group 1 stations ( $-1.0$  and  $-1.2^{\circ}\text{C}$ ) was lower than that of group 2 ( $-1.0$  to  $0^{\circ}\text{C}$ ) and group 3 stations ( $>0^{\circ}\text{C}$  except station 4, with  $-0.3^{\circ}\text{C}$ ) (Fig. 2). Group 1 stations also had lower salinity than other stations, except for two abnormal salinity values (33.2 and 33.4) at stations 4 and 5. In addition, station 15 had significantly lower salinity (33.7) than nearby stations.

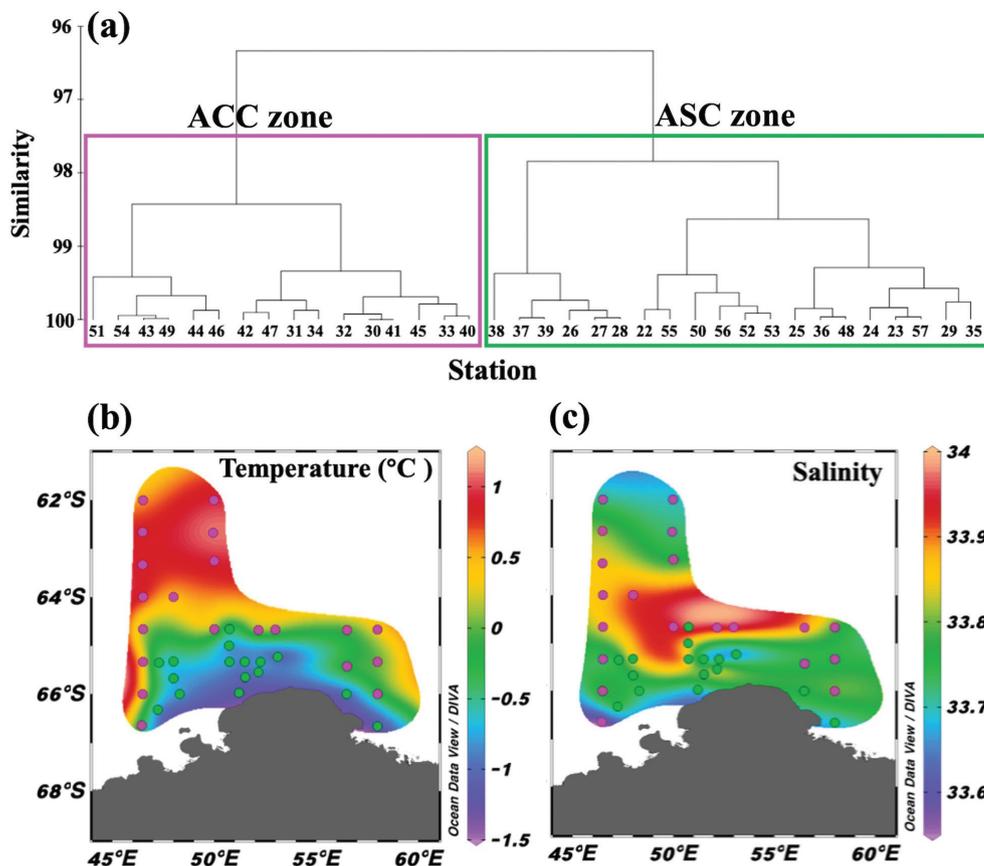
The cluster analysis classified stations in the Cosmonaut Sea into two zones divided by the  $0^{\circ}\text{C}$  isotherm (Fig. 3a, b), which was defined as the front between the Antarctic Slope Current and northern Antarctic Zone. Stations along the continent with low temperature ( $<0^{\circ}\text{C}$ ) were clustered into the ASC zone. Other stations north of the Antarctic Slope Current with temperature  $>0^{\circ}\text{C}$  were classified as the ACC zone. Salinity was high at the frontal stations (Fig. 3c).

**Tintinnid species**

A total of 13 species were identified, including one unidentified species (*Salpingella* sp.) (Fig. 4, Table 1). *Codonellopsis gaussi*, *Laackmanniella naviculaefera*, *Salpingella* sp. and *S. faurei* were the four most frequently occurring species in both the Weddell Sea and Cosmonaut Sea. Nine tintinnid species were identified in the Weddell Sea



**Fig. 2** Cluster analysis of sampling stations 1–21 across the Weddell Gyre. (a) Dendrogram of the station cluster analysis using group-average linkage based on the Bray-Curtis similarity matrix of temperature and salinity. (b) Temperature and salinity data of sampling stations in three groups across the Weddell Gyre.



**Fig. 3** (a) Cluster analysis of sampling stations in the Cosmonaut Sea based on (b) temperature and (c) salinity of the sampling zone. Pink and green points represent ACC zone stations influenced by the Antarctic Circumpolar Current and ASC zone stations covering the Antarctic Slope Current, respectively.

(Supplementary Fig. S1a). Except for *Cymatocylis cristallina* and *Cy. antarctica*, these tintinnid species had OFs >30%. With the highest OF (85.7%), *C. gaussi* also had the largest maximum abundance at 151.2 ind/L. The other six species had maximum abundances ranging 1.9–33.2 ind/L.

In the Cosmonaut Sea, 13 tintinnid species were identified (Supplementary Fig. S1b). These species had OFs >30%, with the exception of *Cy. antarctica*, *Cy. vanhoeffeni* and *S. costata*. With the highest OF (97.2%) amongst all the species, *C. gaussi* had the second maximum highest abundance of 63.0 ind/L. With a high OF of 94.4%, *L. naviculaefera* had a low maximum abundance (<20.0 ind/L).

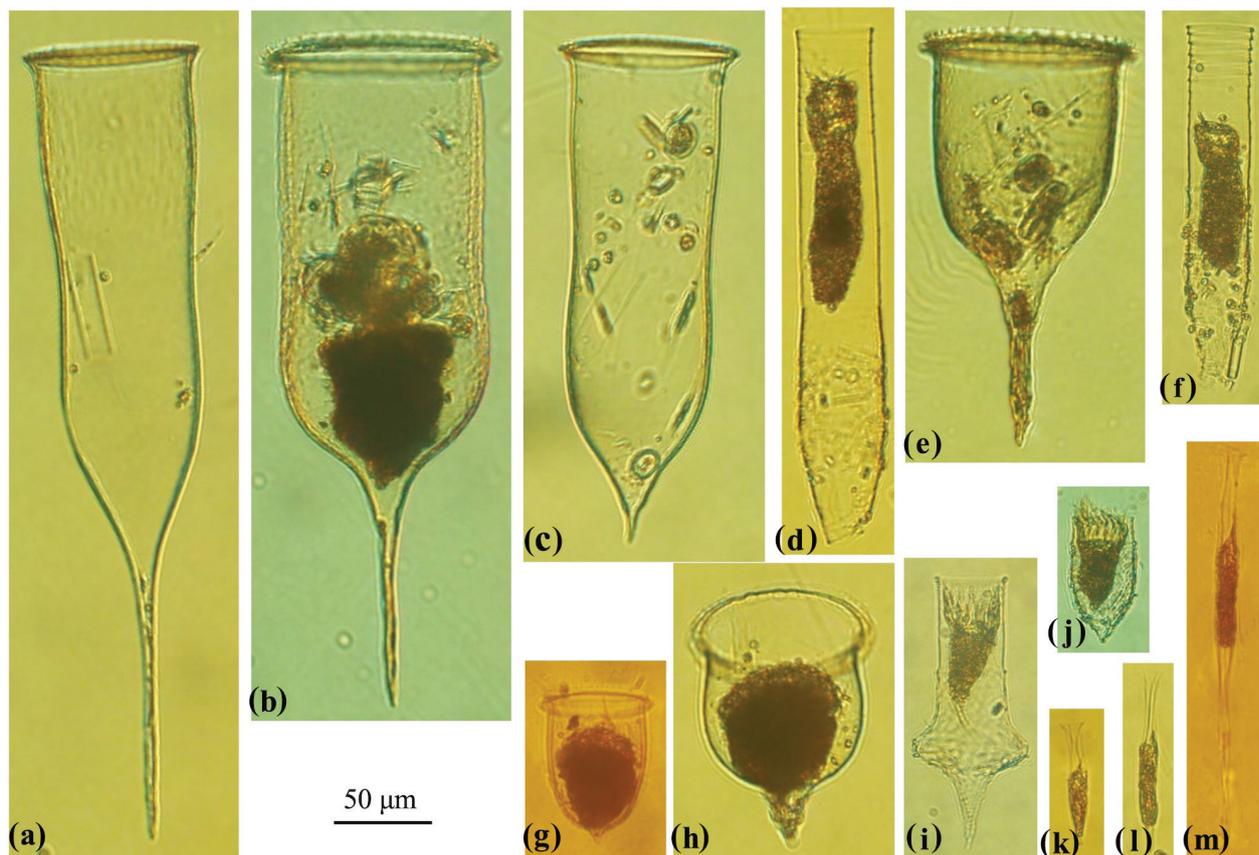
On the basis of variation in the tail bulge of the lorica, *C. gaussi* was divided into three morphological types (Fig. 5). Type I—a visible ring-shaped bulge in the rear of the lorica and a slimline tail—was the most common form. Type II individuals had a shorter tail (even forming a horn) and either a less visible bulge (Fig. 5: first three photographs in Type II) or no bulge at the lower end of the lorica (Fig. 5: last two photographs in Type II). Type III was characterized by a conical lorica without a bulge. The lorica length gradually shortened from Type I to Type III,

but the lorica oral diameter did not differ amongst the three types (Supplementary Fig. S2).

### Tintinnid community in the Weddell Gyre

Tintinnid communities had lower species richness and total abundances at stations in the centre of the Weddell Gyre than at other stations in Transect WG (Fig. 6a, b). Transect WG was divided into four zones on the basis of abundance and species richness at the stations (Fig. 6, Table 2). In the interior of the Weddell Gyre, stations 7–12 had a low average total abundance (8.4 ind/L). At the western front of the gyre, stations 4–6 had the highest average total abundance (104.5 ind/L). At the gyre’s eastern front, stations 13–21 had a moderate average total abundance (36.6 ind/L). In the coastal zone, away from the Weddell Gyre, stations 1–3 had the lowest average total abundance (1.3 ind/L) of the four zones.

Along the Transect WG, tintinnid species with OF >30% had different distributions: *C. gaussi*, *L. naviculaefera* and *L. prolongata* showed lower abundances in the interior of the gyre and higher abundances at the western and eastern



**Fig. 4** Photographs of identified tintinnid species. (a) *Cymatocylis vanhoeffeni*; (b) *Cymatocylis drygalskii*; (c) *Cymatocylis cristallina*; (d) *Laackmanniella prolongata*; (e) *Cymatocylis calyciformis*; (f) *Laackmanniella naviculaefera*; (g) *Cymatocylis antarctica*; (h) *Cymatocylis convallaria*; (i) *Codonellopsis gausi*; (j) *Codonellopsis glacialis*; (k) *Salpingella* sp.; (l) *Salpingella faurei*; (m) *Salpingella costata*.

fronts (Fig. 6c, d); *S. faurei* and *Salpingella* sp. mostly appeared at the eastern front (Fig. 6e); *Cy. drygalskii* and *Cy. convallaria* appeared in four zones, with similar abundances that were lower than other species (Fig. 6f). In addition, Transect WG had two anomalous stations. Station 9 was located in the interior zone but had a high tintinnid abundance (33.5 ind/L) and species richness (eight species); these values were notably higher than at neighbouring stations in the interior zone. Station 16 was located at the eastern front but had a much lower tintinnid abundance (5.4 ind/L) than at neighbouring eastern front stations (Fig. 6b).

Although similar tintinnid species occurred in both the interior zone and two frontal zones, their abundance proportions varied in different zones (Table 2). Four tintinnid species (*C. gausi*, *L. naviculaefera*, *Salpingella* sp. and *S. faurei*) dominated the tintinnid community in three zones, with abundance proportions higher than 90%. *Codonellopsis gausi* showed a decreasing proportion of abundance from the western front (93.2%) to the eastern front (34.2%); Type I *C. gausi* had a lower abundance proportion trend from the western front (63.2%) to the

eastern front (31.5%), whilst Type II *C. gausi* had the same lower abundance proportion trend from the west front (30.0%) to the east front (1.9%). The abundance proportions of *L. naviculaefera*, *S. faurei* and *Salpingella* sp. increased from the western front (3.2, 1.9 and 1.1%, respectively) to the eastern front (16.1, 24.6 and 19.4%, respectively).

The coastal zone had different tintinnid abundance proportions compared with the other three zones (Table 2). Type II *C. gausi* did not occur in the coastal zone. *C. gausi* comprised a smaller proportion of the tintinnid community in the coastal zone than in other zones. However, Types I and III *C. gausi* appeared in high proportions (>10.0%) in the coastal zone. The abundance proportions of *Cy. convallaria* and *Cy. drygalskii* (37.9 and 9.0%, respectively) were greater in the coastal zone than in the other three zones.

#### **Tintinnid community in the Antarctic Slope Current in the Cosmonaut Sea**

In the Cosmonaut Sea, the tintinnid community in the ACC and ASC zones varied with water mass. In general,

there were higher average abundances and richness in the ACC zone than in the ASC zone. Total abundances were high at stations in the frontal zone between the ACC and ASC zones (Fig. 7, Table 3).

Species richness was higher in the ACC zone than the ASC zone (Fig. 7a). Ten tintinnid species with OF > 30% had distinct distributions in the ACC and ASC zones (Fig. 7). *Cymatocylis drygalskii* occurred mainly in the ASC zone, except for one station (station 26) in the ACC zone (Fig. 7o). Three species (*Cy. convallaria*, *C. calyciformis* and *C. glacialis*) were found in higher abundances in the ACC zone than in the ASC zone (Fig. 7c–e). The remaining six species (*Cy. cristallina*, *L. prolongata*, *S. faurei*, *C. gaussi*, *L. naviculaefera* and *Salpingella* sp.) were found in both the ASC and ACC zones and had peak abundances near the front (Fig. 7f–n). Collectively, the total tintinnid

abundance showed peak values at station 23 (81.3 ind/L), station 36 (98.2 ind/L) and station 55 (75.8 ind/L) near the front (Fig. 7b).

The ASC zone had lower average total abundances than in the ACC zone (Table 3). The four most frequent species (*C. gaussi*, *L. naviculaefera*, *Salpingella* sp. and *S. faurei*) occupied most of the tintinnid abundance in both water masses (abundance proportions of 78.8 and 88.6% in the ASC and ACC zones, respectively). The average abundance and average proportion of *Cy. drygalskii* were higher in the ASC zone (1.1 ind/L and 4.5%) than in the ACC zone (0.3 ind/L and 0.9%). *Cymatocylis convallaria*, *C. glacialis* and *Cy. calyciformis* were the endemic species in the ACC zone, with significantly higher abundance proportions (15.7%) in the ACC zone than in the ASC zone (2.7%).

For *C. gaussi*, the abundance proportion was higher in the ASC zone (35.1%) than in the ACC zone (25.6%). The distributions of the three types of *C. gaussi* were different: the abundance proportions of Type II and Type III were higher in the ASC zone (10.0 and 14.6%, respectively) than in the ACC zone (3.4 and 8.4%, respectively), whilst the proportion of Type I was lower in the ASC zone (10.5%) than in the ACC zone (13.8%).

**Table 1** Lorica oral diameter and lorica length of tintinnids (average ± standard deviation, n = 20).

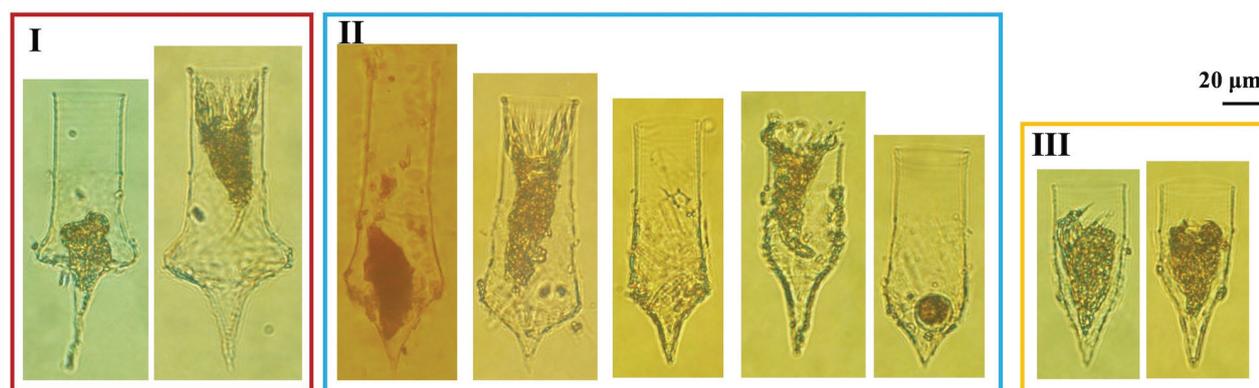
| Species                                    | Lorica oral diameter (µm) | Lorica length (µm) |
|--|---------------------------|--------------------|
| <i>Codonellopsis glacialis</i>             | 27.8 ± 1.1                | 60.3 ± 5.5         |
| <i>Codonellopsis gaussi</i>                | 30.5 ± 2.3                | 99.4 ± 26.8        |
| <i>Cymatocylis drygalskii</i>              | 83.2 ± 8.7                | 240.4 ± 21.7       |
| <i>Cymatocylis cristallina</i>             | 90.5 ± 6.8                | 278.9 ± 31.8       |
| <i>Cymatocylis vanhoeffeni</i>             | 74.6 ± 6.9                | 409.8 ± 50.1       |
| <i>Cymatocylis convallaria</i>             | 79.9 ± 7.3                | 135.7 ± 13.7       |
| <i>Cymatocylis calyciformis</i>            | 87.0 ± 5.2                | 225.0 ± 61.9       |
| <i>Cymatocylis antarctica</i> <sup>a</sup> | 44.6 ± 3.2                | 68.9 ± 3.1         |
| <i>Laackmanniella naviculaefera</i>        | 28.9 ± 2.1                | 167.1 ± 46.3       |
| <i>Laackmanniella prolongata</i>           | 30.9 ± 2.5                | 212.4 ± 39.2       |
| <i>Salpingella</i> sp.                     | 8.5 ± 1.3                 | 57.0 ± 7.1         |
| <i>Salpingella faurei</i>                  | 10.3 ± 1.7                | 93.2 ± 22.2        |
| <i>Salpingella costata</i> <sup>a</sup>    | 17.7 ± 0.2                | 201.1 ± 1.1        |

<sup>a</sup>Species with less than 20 individuals measured.

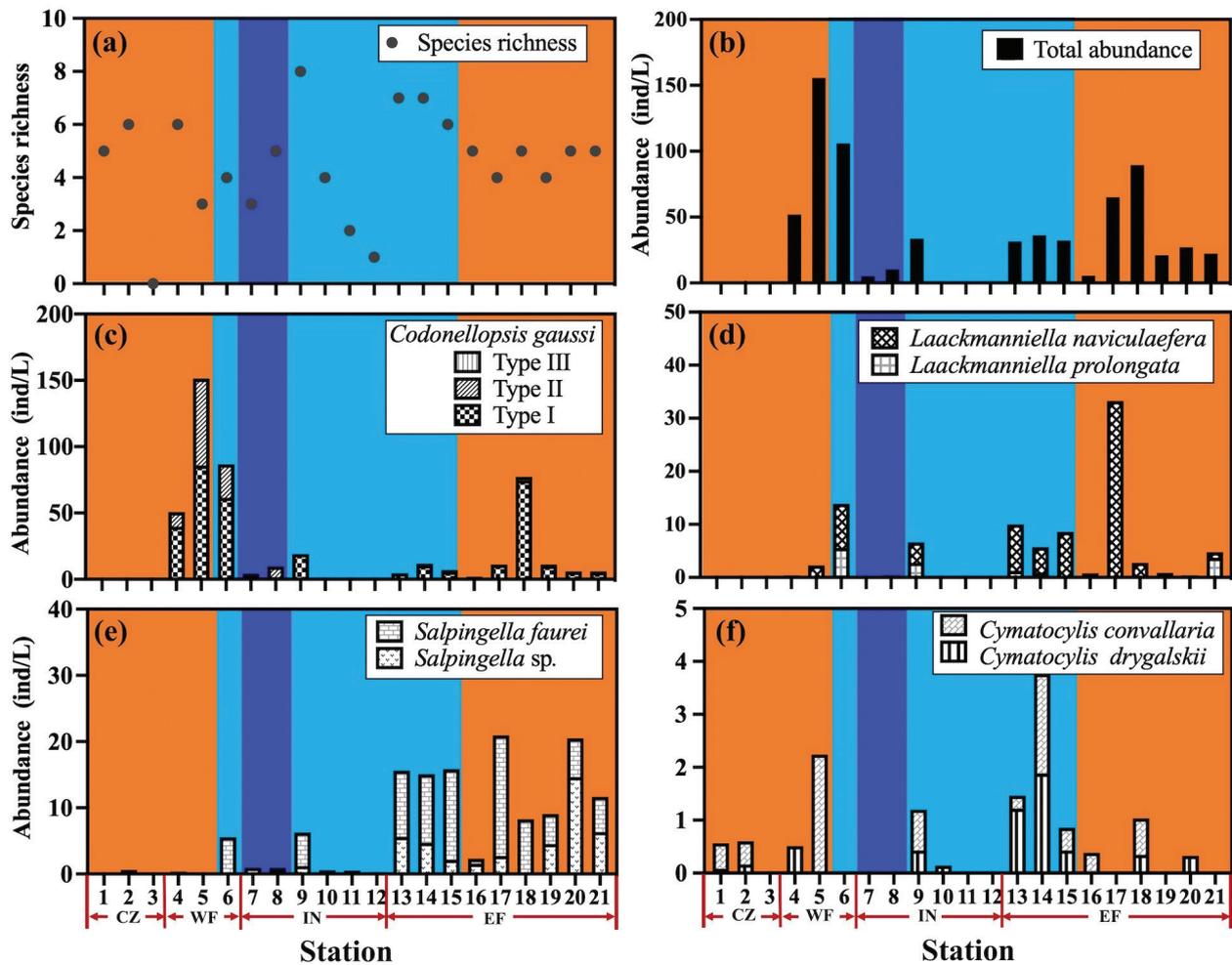
**Discussion**

In our study, the detection limit of tintinnid abundance was 0.25 cells/L, and only near-surface waters were sampled. Therefore, the following discussion concerning tintinnid occurrence is limited to the surface waters and species with abundances exceeding 0.25 ind/L.

In the present study, the tintinnid abundance range in austral summer in the Weddell Sea (0–155.7 ind/L) was



**Fig. 5** Photographs of polymorphic *Codonellopsis gaussi* types. I: individuals with a prominent ring-shaped bulge in the rear of the lorica and a slimline tail; II: individuals with a less pronounced ring-shaped bulge at the lower end of the lorica; and III: individuals with a conical lorica, almost no bulge at the lower end of the lorica, and a significantly shorter body than the other two types.



**Fig. 6** Tintinnid (a) species richness and (b) abundance; total abundances of (c) three types of *Codonellopsis gaussi*, (d) *Laackmanniella naviculaefera* and *Laackmanniella prolongata*, (e) *Salpingella faurei* and *Salpingella* sp. and (f) *Cymatocyclus convallaria* and *Cymatocyclus drygalskii* along Transect WG in the Weddell Sea. Stations 1–3 were in the coastal zone far from the Weddell Gyre (CZ). Stations 4–6 were at the western front of the gyre (WF). Stations 7–12 were in the interior of the gyre (IN). Stations 13–21 were at the gyre’s eastern front (EF).

**Table 2** Average abundances of all species and abundance proportions in four zones along Transect WG.

| Species                             | Average abundance (ind/L) |                 |                 |                 | Abundance proportion (%) |                 |                 |                 |
|-------------------------------------|---------------------------|-----------------|-----------------|-----------------|--------------------------|-----------------|-----------------|-----------------|
|                                     | CZ <sup>a</sup>           | WF <sup>b</sup> | IN <sup>c</sup> | EF <sup>d</sup> | CZ <sup>a</sup>          | WF <sup>b</sup> | IN <sup>c</sup> | EF <sup>d</sup> |
| <i>Salpingella</i> sp.              | 0.3 ± 0.3                 | <0.1            | 0.5 ± 0.5       | 4.7 ± 4.3       | 18.6 ± 14.6              | 1.1 ± 0         | 14.1 ± 12.3     | 19.4 ± 16.6     |
| <i>Salpingella faurei</i>           | <0.1                      | 1.9 ± 3.2       | 1.0 ± 2.0       | 8.5 ± 5.2       | 3.2 ± 4.5                | 1.9 ± 2.9       | 39.0 ± 40.7     | 24.6 ± 9.8      |
| <i>Codonellopsis gaussi</i> I       | 0.2 ± 0.1                 | 62.3 ± 23.0     | 3.8 ± 7.51      | 14.3 ± 22.8     | 12.3 ± 5.5               | 63.2 ± 1.2      | 20.2 ± 23.1     | 31.5 ± 22.0     |
| <i>Codonellopsis gaussi</i> II      | -                         | 33.8 ± 28.3     | 1.6 ± 2.9       | 0.7 ± 0.9       | -                        | 30.0 ± 1.1      | 18.5 ± 30.4     | 1.9 ± 1.6       |
| <i>Codonellopsis gaussi</i> III     | 0.2 ± 0                   | -               | -               | <0.1            | 13.2 ± 4.9               | -               | -               | 0.8 ± 2.4       |
| <i>Cymatocyclus drygalskii</i>      | 0.12 ± 0.1                | 0.2 ± 0.3       | <0.1            | 0.5 ± 0.7       | 9.0 ± 0.9                | 0.3 ± 1.0       | 3.2 ± 7.3       | 1.3 ± 1.9       |
| <i>Cymatocyclus convallaria</i>     | 0.5 ± 0.03                | 0.8 ± 1.3       | 0.1 ± 0.3       | 0.4 ± 0.6       | 37.9 ± 17.2              | 0.5 ± 0.1       | 0.4 ± 0.9       | 1.7 ± 2.6       |
| <i>Laackmanniella prolongata</i>    | -                         | 1.9 ± 3.2       | 0.5 ± 1.1       | 0.7 ± 1.2       | -                        | 1.9 ± 3.0       | 1.7 ± 3.3       | 2.7 ± 5.4       |
| <i>Laackmanniella naviculaefera</i> | -                         | 3.6 ± 4.2       | 0.7 ± 1.6       | 6.7 ± 10.5      | -                        | 3.2 ± 4.1       | 2.7 ± 4.5       | 16.1 ± 16.5     |
| Other species with OF <30%          | <0.1                      | -               | <0.1            | -               | 5.8 ± 3.6                | -               | 0.2 ± 0.5       | -               |
| All species                         | 1.3 ± 0.5                 | 104.5 ± 51.9    | 8.4 ± 12.9      | 36.6 ± 25.4     | 100.0                    | 100.0           | 100.0           | 100.0           |

<sup>a</sup> Coastal zone far from the Weddell Gyre (stations 1–3). <sup>b</sup> Western front of the gyre (stations 4–6). <sup>c</sup> Interior of the gyre (stations 7–12). <sup>d</sup> The gyre’s eastern front (stations 13–21).

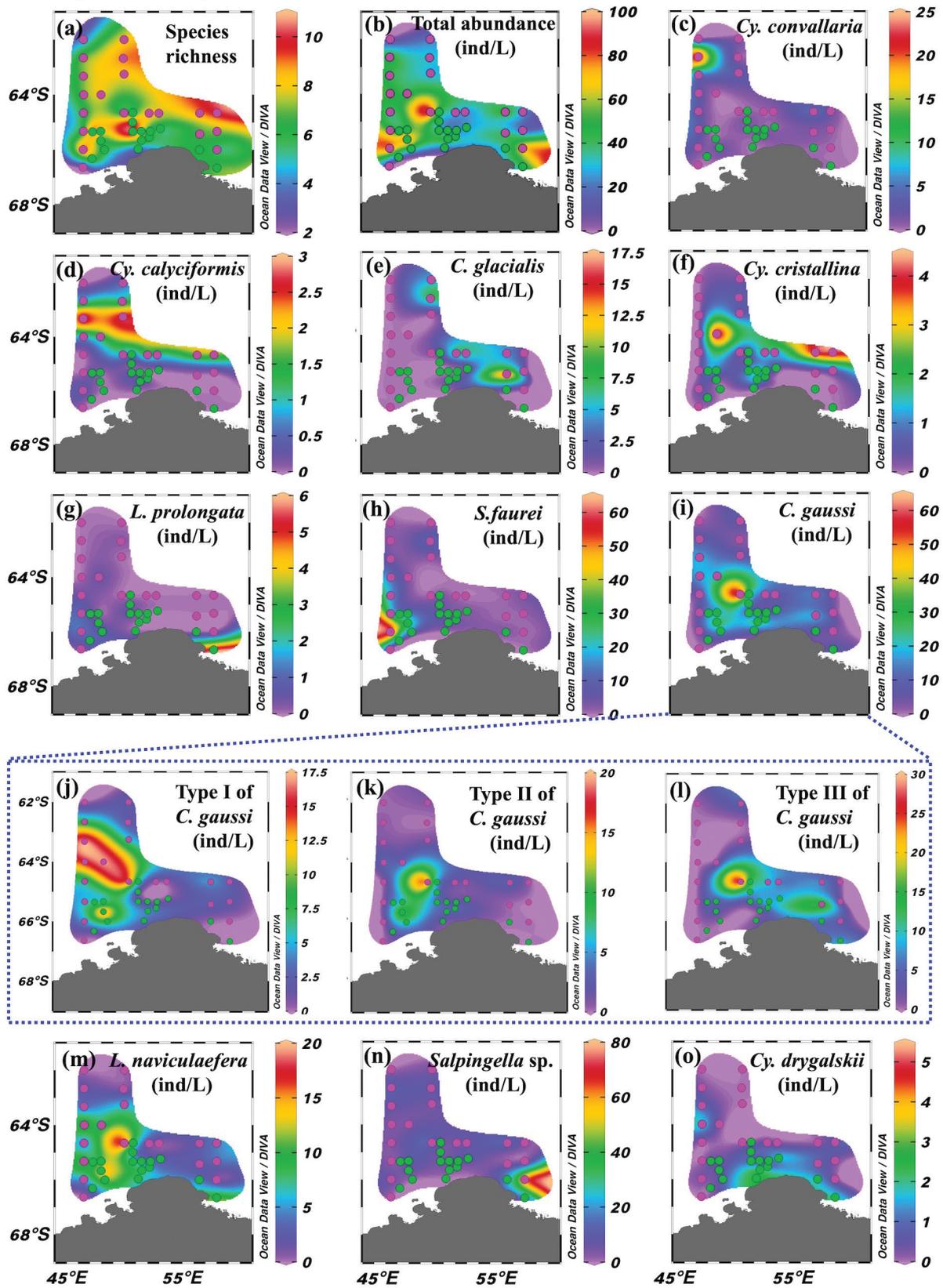


Fig. 7 (a) Species richness, (b) total abundance and (c-o) abundance (ind/L) of individual tintinnid species in the Cosmonaut Sea.

**Table 3** Average abundances of all species and abundance proportions for two station zones.

| Species                             | Average abundance (ind/L)    |                              | Abundance proportion (%)     |                              |
|-------------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|
|                                     | ACC <sup>a</sup><br>stations | ASC <sup>b</sup><br>stations | ACC <sup>a</sup><br>stations | ASC <sup>b</sup><br>stations |
| <i>Codonellopsis glacialis</i>      | 2.1 ± 4.2                    | <0.1                         | 6.8 ± 12.1                   | 0.2 ± 0.7                    |
| <i>Salpingella</i> sp.              | 9.0 ± 15.6                   | 5.2 ± 5.0                    | 19.1 ± 19.8                  | 15.5 ± 14.8                  |
| <i>Salpingella faurei</i>           | 7.9 ± 14.6                   | 6.3 ± 7.8                    | 22.7 ± 26.4                  | 16.5 ± 12.2                  |
| <i>Codonellopsis gaussi</i> I       | 5.9 ± 6.0                    | 3.6 ± 3.9                    | 13.8 ± 12.1                  | 10.5 ± 8.0                   |
| <i>Codonellopsis gaussi</i> II      | 1.8 ± 4.1                    | 3.4 ± 3.0                    | 3.4 ± 4.5                    | 10.0 ± 5.4                   |
| <i>Codonellopsis gaussi</i> III     | 3.8 ± 7.7                    | 4.4 ± 3.3                    | 8.4 ± 12.4                   | 14.6 ± 12.1                  |
| <i>Cymatocylis drygalskii</i>       | 0.3 ± 0.5                    | 1.1 ± 1.3                    | 0.9 ± 1.4                    | 4.5 ± 6.4                    |
| <i>Cymatocylis cristallina</i>      | 0.8 ± 1.5                    | 0.5 ± 0.8                    | 2.6 ± 4.8                    | 1.7 ± 3.0                    |
| <i>Cymatocylis convallaria</i>      | 2.8 ± 5.3                    | 0.6 ± 0.6                    | 6.5 ± 10.8                   | 2.2 ± 2.2                    |
| <i>Cymatocylis calyciformis</i>     | 0.8 ± 0.9                    | <0.1                         | 2.4 ± 2.9                    | 0.3 ± 0.5                    |
| <i>Laackmanniella prolongata</i>    | 0.2 ± 0.4                    | 0.6 ± 1.4                    | 1.3 ± 4.1                    | 1.6 ± 3.4                    |
| <i>Laackmanniella naviculaefera</i> | 4.6 ± 4.8                    | 6.8 ± 3.5                    | 11.4 ± 11.2                  | 21.5 ± 8.0                   |
| Other species with OF <30%          | 0.2 ± 0.3                    | 0.3 ± 0.3                    | 0.8 ± 1.3                    | 0.8 ± 0.9                    |
| All species                         | 40.2 ± 26.1                  | 33.1 ± 16.6                  | 100.0                        | 100.0                        |

<sup>a</sup>Antarctic Circumpolar Current. <sup>b</sup>Antarctic Slope Current.

within the range of 0–859 ind/L in summer reported in a previous study (Boltovskoy et al. 1989). Some studies reported tintinnid abundance ranges of 1–445 ind/L in autumn (Buck et al. 1992) and 1–440 ind/L in austral spring (Garrison & Buck 1989). However, some authors reported high summer tintinnid abundances of 3000 ind/L (Buck & Garrison 1983) and 6500 ind/L (Trifoglio et al. 2023) in the Weddell Sea. In the Cosmonaut Sea, our maximum tintinnid abundance of 98.2 ind/L was lower than the abundance reported by Li et al. (2022) of 586 ind/L.

### Tintinnid community in different water masses

To our knowledge, the present study is the first to document a difference in plankton communities between the Weddell Gyre centre and the surrounding zones. Although several tintinnid community studies have filtered large volumes (5–2000 L) of surface waters using small nets (mesh size 20 or 26 µm) in the Weddell Sea (Buck & Garrison 1983; Boltovskoy et al. 1989; Garrison & Buck 1989; Gowing & Garrison 1991, 1992; Nöthig & Gowing 1991), their transects (stations) were meridional and were located west of 30°W (Supplementary Fig. S3). These previous studies did not analyse the differences in zooplankton between the centre and the edges of the Weddell Gyre, which is a huge and complex water mass roughly located between 60°W and 30°E (Deacon 1979).

We found that *C. gaussi*, *L. naviculaefera*, *Salpingella* sp. and *S. faurei* were the four dominant species in the Transect WG. Previous studies found that *C. gaussi* dominated in a narrow sampling zone in the northern–central

Weddell Sea, at approximately 45–55°W, which corresponds to the eastern front zone in our study (Boltovskoy et al. 1989; Alder & Boltovskoy 1991). In the present study, we further found that *C. gaussi* made a significantly higher contribution to the total abundance in the west front zone than the eastern front zone of the Weddell Gyre. The contribution of *C. gaussi* and the other three main species—*L. naviculaefera*, *Salpingella* sp. and *S. faurei*—to the total abundance showed opposite trends in the eastern and western front zones of Transect WG. This phenomenon may be explained by the gyre rotation. The water moves from the eastern front to the western front, forming a semicircle along the gyre trajectory. During this process, the dominance of these species changes in accordance with their adaptation to environmental variation associated with latitudinal change and mixing with coastal waters. This process is similar to the tintinnid community variation in different parts of subtropical gyres (Li, Tarran et al. 2023).

The coastal zone in Transect WG was a mixed area that was influenced by the Antarctic Circumpolar Current, Antarctic Slope Current and Weddell Gyre (Fig. 1a). The low abundance of total tintinnids in the coastal zone might be because the mixed water was not suitable for many of the species that originated from these individual water masses. A study of waters around the Antarctic Peninsula found that *Cy. convallaria* was one of the dominant species (Li, Liang et al. 2023), which is consistent with the high abundance proportion of *Cy. convallaria* (37.9%) in the coastal zone of Transect WG in our study. The lower abundance proportions of *C. gaussi*, *L. naviculaefera*, *Salpingella*

sp. and *S. faurei* in the coastal zone might be because of the increased contributions of species from the Antarctic Slope Current (*Cy. drygalskii*) and species from the Antarctic Circumpolar Current (*Cy. convallaria*).

The anomalous results from two stations in the transect may be explained by disturbance of general circulation patterns. The high tintinnid abundance and species richness at station 9 might be caused by filaments from the north limb of the Weddell Gyre (Fahrbach et al. 2011; Reeve et al. 2019), whilst the low tintinnid abundance at station 16 might be due to the northern migration of fronts led by topography elevation and Maud Rise upwelling (Jena et al. 2019).

Our sampling stations in the Cosmonaut Sea were in the convergence area of the Antarctic Slope Current and the Antarctic Circumpolar Current (Comiso & Gordon 1996; Fig. 1b). We found a high tintinnid abundance at the intersection of these two water masses, which is similar to the findings of a study in the Ross Sea (Wang, Xu et al. 2022). Liang et al. (2020) showed that *C. glacialis* and *Cy. calyciformis* were abundant near the Polar Front, whilst *Cy. convallaria* occurred south of the Polar Front. In our study, the abundance proportions of *Cy. convallaria*, *C. glacialis* and *Cy. calyciformis* were lower in the ASC zone than in the ACC zone in the Cosmonaut Sea. We speculate that these three species might be entrained from the ACC zone in the north and, therefore, showed low contributions in the ASC zone. Similarly, *C. glacialis* and *Cy. calyciformis* were not detected in the Weddell Gyre because of the weak influence of the Antarctic Circumpolar Current on the Weddell Gyre.

Tintinnid diversity in relation to water masses has been reported worldwide, especially with regard to its uses in indicating the division of inshore and offshore currents (Sitran et al. 2007; Polat et al. 2019). In our study, *Cy. drygalskii* was endemic in the ASC zone and occasionally appeared in the ACC zone. This phenomenon is consistent with previous studies. Alder & Boltovskoy (1991) showed that *Cy. drygalskii* is one of the dominant species in the shelf and mostly ice-covered areas of the southernmost Weddell Sea and the Bellingshausen Sea. Similarly, Liang et al. (2018) discovered that *Cy. drygalskii* is more abundant at stations closer to shore in Prydz Bay, and Trifoglio et al. (2023) also found that *Cy. drygalskii* is limited to shelf waters. *Cymatocylis drygalskii* could also be advected from coastal waters into offshore waters in the north. Therefore, we recommend *Cy. drygalskii* as an indicator of the Antarctic Slope Current.

### **Codonellopsis gaussi polymorphism in different water masses**

For most tintinnid species, individuals of the same species have similar lorica forms and lorica oral diameters (Dolan

et al. 2006). Individuals of the same genus are classified as different species on the basis of the shapes and sizes of loricae, allowing for some morphological differences amongst individuals in the same species (Williams et al. 1994). However, lorica polymorphism is seen in some tintinnid species such as *C. gaussi*, which is an endemic species in the Southern Ocean (Dolan et al. 2012). As the most common species in the Weddell Sea, *C. gaussi* was first recorded by Laackmann (1907); subsequently, many other *C. gaussi* forma (like *coxiella*, *cylindroconical/cylindrica*, *globosa* and *typica*) were reported in later studies (Laackmann 1910; Balech 1973; Sassi & Melo 1986; Alder 1995). Our Type I and Type III *C. gaussi* are located at the two extremes of the spectrum presented in Alder's figure IV.4 (1995), whilst our Type II *C. gaussi* is in between the two extremes. Some of our Type II *C. gaussi* specimens were identified as *C. glacilis* in Fig. 8 of Dolan et al. (2022).

Different morphologies of *C. gaussi* coexist in the waters near the Antarctic Peninsula and the Weddell Sea (Alder & Boltovskoy 1991), Ross Sea (Dolan et al. 2022) and Amundsen Sea (Dolan et al. 2013), but the distribution of those morphologies has never been clearly described. Dolan et al. (2012) speculated that polymorphism may be associated with the occurrence of population growth in rapid, short-lived bursts with a consequence of cell division rates exceeding normal lorica-formation rates. However, in the Amundsen Sea, the occurrence of different *C. gaussi* morphologies shows no clear relationship with the composition of the microphytoplankton (Dolan et al. 2013). In our research, we found that the abundance contribution of different morphological types of *C. gaussi* was related to water masses. Type I *C. gaussi* appeared at most stations. Type II *C. gaussi* had a higher percentage in the ASC zone of the Cosmonaut Sea and in the interior and western front of Transect WG. Type III *C. gaussi* comprised a higher percentage in the coastal zone of Transect WG and the ASC zone of the Cosmonaut Sea. Our results support the idea of Dolan et al. (2012) that growth conditions cause the different abundance proportions of *C. gaussi* morphological types. However, contrary to the proposition of Dolan et al. (2012) that good growth conditions cause higher proportions of Types II and III, we propose that there might be a higher proportion of Type III when this species is in a status of stress.

### **Implication of tintinnids to different gyres in the Southern Ocean**

Our finding that tintinnid abundance was lower in the centre of the Weddell Gyre was consistent with the low productivity in the gyre centre (Vernet et al. 2019). In the Weddell Gyre, divergence in the interior area is steered by cyclonic circulation and induces deep water upwelling (Marshall & Speer 2012), which causes low temperature

water to be transported to the surface. Frontal zones in the Weddell Sea show a positive correlation between productivity and biomass (Park et al. 2010). The distribution of tintinnids in our study also conformed to this trend. However, the west front had a higher total tintinnid abundance than the eastern front, which might be because the west front zone was near the ice-edge zone, and the ice-edge blooms contribute to the growth of surface biota (Daly & Macaulay 1991; Massom et al. 2006). The spatial distribution of other phytoplankton and zooplankton taxa in different parts of the Weddell Gyre has not been studied (Vernet et al. 2019). The distribution of phytoplankton and zooplankton might be similar to that of tintinnids in our study because these taxa are influenced by the same hydrological transport and mixing processes.

The Ross Sea is another similar important area with a gyre in the Antarctic Zone. Tintinnid studies in the Ross Sea have focused on Terra Nova Bay (Monti-Birkenmeier et al. 2022) and waters south of Terra Nova Bay (Wang, Wang et al. 2022), which are outside the Ross Gyre. These studies showed that *C. gaussi* also dominates the tintinnid communities in the waters outside Ross Gyre in the Ross Sea. We speculate that the tintinnid community in different parts of the Ross Gyre would be similar to that of the Weddell Gyre.

## Conclusions

This study was the first to evaluate the tintinnid distribution in surface waters along a west–east transect across the Weddell Gyre and an area covering both the Antarctic Circumpolar Current and the Antarctic Slope Current in the Cosmonaut Sea. In the Weddell Gyre, the tintinnid community showed obvious variations between the centre of the gyre and its frontal zones. The rotation of the gyre might cause tintinnid community spatial heterogeneity. In the Cosmonaut Sea, the tintinnid community had a higher abundance of *Cy. drygalskii* in the Antarctic Slope Current than the Antarctic Circumpolar Current. Therefore, *Cy. drygalskii* could serve as an indicator of the Antarctic Slope Current, which would be useful in studies of how zooplanktonic biogeography is changing in the Southern Ocean as it warms. The abundance distributions of polymorphic individuals of *C. gaussi* in the Weddell and Cosmonaut Seas suggested that Type III mainly occurred in the coastal waters, where this species might be in a state of stress.

## Acknowledgements

The authors thank the 38th Chinese National Antarctic Research Expedition for providing logistical support and

environmental data. The authors also thank Kelly Zammit, from Liwen Bianji (Edanz), for editing the English draft of this manuscript.

## Funding

This study was supported by the Impact and Response of Antarctic Seas to Climate Change project (grant no. IRASCC 01-02-01D), the National Natural Science Foundation of China (grant nos. 41706192, 41806178 and 42206258) and the Shandong Provincial Natural Science Foundation (grant no. ZR2022QD022).

## Disclosure statement

The authors report no conflict of interest.

## References

- Alder V.A. 1995. *Ecología y sistemática de Tintinnina (Protozoa, Ciliata) y microzoopláncteres asociados de aguas antárticas. (Ecology and systematics of Tintinnina [Protozoa, Ciliata] and associated microzooplankton in Antarctic waters.)* PhD dissertation, University of Buenos Aires.
- Alder V.A. & Boltovskoy D. 1991. The ecology and biogeography of tintinnid ciliates in the Atlantic sector of the Southern Ocean. *Marine Chemistry* 35, 337–346, doi: 10.1016/S0304-4203(09)90026-3.
- Balech E. 1973. *Segunda contribución al conocimiento del microplancton del Mar de Bellingshausen. (Second contribution to our knowledge of the microplankton of the Bellingshausen Sea.)* *Contribucion del Instituto Antártico Argentino* 107. Buenos Aires: National Antarctic Directorate.
- Boltovskoy D., Alder V.A. & Spinelli F. 1989. Summer Weddell sea microplankton: assemblage structure, distribution and abundance, with special emphasis on the Tintinnina. *Polar Biology* 9, 447–456, doi: 10.1007/BF00443232.
- Buck K.R. & Garrison D.L. 1983. Protists from the ice-edge region of the Weddell Sea. *Deep-Sea Research Part A* 30, 1261–1277, doi: 10.1016/0198-0149(83)90084-5.
- Buck K.R., Garrison D.L. & Hopkins T.L. 1992. Abundance and distribution of tintinnid ciliates in an ice edge zone during the austral autumn. *Antarctic Science* 4, 3–8, doi: 10.1017/S0954102092000038.
- Comiso J.C. & Gordon A.L. 1996. Cosmonaut polynya in the Southern Ocean: structure and variability. *Journal of Geophysical Research—Oceans* 101, 18297–18313, doi: 10.1029/96JC01500.
- Daly K. & Macaulay M. 1991. Influence of physical and biological mesoscale dynamics on the seasonal distribution and behavior of *Euphausia superba* in the Antarctic marginal ice zone. *Marine Ecology Progress Series* 79, 37–66, doi: 10.3354/meps079037.
- Deacon G.E.R. 1979. The Weddell gyre. *Deep-Sea Research Part A* 26, 981–995, doi: 10.1016/0198-0149(79)90044-X.

- Dolan J.R., Jacquet S. & Torr eton J.-P. 2006. Comparing taxonomic and morphological biodiversity of tintinnids (planktonic ciliates) of New Caledonia. *Limnology and Oceanography* 51, 950–958, doi: 10.4319/lo.2006.51.2.0950.
- Dolan J.R., Jin Yang E., Hoon Lee S. & Young Kim S. 2013. Tintinnid ciliates of Amundsen Sea (Antarctica) plankton communities. *Polar Research* 32, article no. 19784, doi: 10.3402/polar.v32i0.19784.
- Dolan J.R., Pierce R.W., Yang E.J. & Kim S.Y. 2012. Southern Ocean biogeography of tintinnid ciliates of the marine plankton. *Journal of Eukaryotic Microbiology* 59, 511–519, doi: 10.1111/j.1550-7408.2012.00646.x.
- Dolan J.R., Son W., La H.S., Park J. & Yang E.J. 2022. Tintinnid ciliates (marine microzooplankton) of the Ross Sea. *Polar Research* 41, article no. 8382, doi: 10.33265/polar.v41.8382.
- Fahrbach E., Hoppema M., Rohardt G., Boebel O., Klatt O. & Wisotzki A. 2011. Warming of deep and abyssal water masses along the Greenwich meridian on decadal time scales: the Weddell gyre as a heat buffer. *Deep-Sea Research Part II* 58, 2509–2523, doi: 10.1016/j.dsr2.2011.06.007.
- Fonda Umani S., Monti M., Cataletto B. & Budillon G. 2011. Tintinnid distributions in the Strait of Magellan (Chile). *Polar Biology* 34, 1285–1299, doi: 10.1007/s00300-011-0972-7.
- Friedenberg L.E., Bollens S.M. & Rollwagen-Bollens G. 2012. Feeding dynamics of larval Pacific herring (*Clupea pallasii*) on natural prey assemblages: the importance of protists: larval herring feeding on protists. *Fisheries Oceanography* 21, 95–108, doi: 10.1111/j.1365-2419.2011.00611.x.
- Garrison D.L. 1991. An overview of the abundance and role of protozooplankton in Antarctic waters. *Journal of Marine Systems* 2, 317–331, doi: 10.1016/0924-7963(91)90039-W.
- Garrison D.L. & Buck K.R. 1989. Protozooplankton in the Weddell Sea, Antarctica: abundance and distribution in the ice-edge zone. *Polar Biology* 9, 341–351, doi: 10.1007/BF00442524.
- Gowing M.M. & Garrison D.L. 1991. Austral winter distributions of large tintinnid and large sarcodinid protozooplankton in the ice-edge zone of the Weddell/Scotia seas. *Journal of Marine Systems* 2, 131–141, doi: 10.1016/0924-7963(91)90019-Q.
- Gowing M.M. & Garrison D.L. 1992. Abundance and feeding ecology of larger protozooplankton in the ice edge zone of the Weddell and Scotia seas during the austral winter. *Deep-Sea Research Part A* 39, 893–919, doi: 10.1016/0198-0149(92)90128-G.
- Hodgson D.A., Graham A.G.C., Roberts S.J., Bentley M.J., Cofaigh C. ., Verleyen E., Vyverman W., Jomelli V., Favier V., Brunstein D., Verfaillie D., Colhoun E.A., Saunders K.M., Selkirk P.M., Mackintosh A., Hedding D.W., Nel W., Hall K., McGlone M.S., Van der Putten N., Dickens W.A. & Smith J.A. 2014. Terrestrial and submarine evidence for the extent and timing of the Last Glacial Maximum and the onset of deglaciation on the maritime-Antarctic and sub-Antarctic islands. *Quaternary Science Reviews* 100, 137–158, doi: 10.1016/j.quascirev.2013.12.001.
- Hu T., Wang Z., Liu W. & Lin X. 2022. Taxonomy and phylogeny of two tintinnid ciliates of *Leptotintinnus* (Protista, Ciliophora, Choreotrichida) combining the loricae, cytological, ontogenetic features, and barcoding genes. *Frontiers in Marine Science* 9, article no. 847600, doi: 10.3389/fmars.2022.847600.
- Jena B., Ravichandran M. & Turner J. 2019. Recent reoccurrence of large open-ocean polynya on the Maud Rise Seamount. *Geophysical Research Letters* 46, 4320–4329, doi: 10.1029/2018GL081482.
- Kim S.Y., Choi J.K., Dolan J.R., Shin H.C., Lee S. & Yang E.J. 2013. Morphological and ribosomal DNA-based characterization of six Antarctic ciliate 5 morphospecies from the Amundsen Sea with phylogenetic analyses. *Journal of Eukaryotic Microbiology* 60, 497–513, doi: 10.1111/jeu.12057.
- Laackmann H. 1907. Antarktische Tintinnen. (Antarctic Tintinnina.) *Zoologischer Anzeiger* 31, 235–239.
- Laackmann H. 1910. Die Tintinnideen der deutschen S udpolar Expedition 1901–1902. (The tintinnids of the German South Pole Expedition 1901–1902.) *Deutsche S udpolar-Expedition 1901–1903, 11 (Zoologie III)*, 340–496.
- Li H., Liang C., Yang G., Wang C. & Zhang W. 2023. Spatial distribution of planktonic ciliates in waters around the northeastern Antarctic Peninsula and the South Orkney Plateau. *Polar Biology*, 623–637, doi: 10.1007/s00300-023-03152-6.
- Li H., Tarran G.A., Dall’Olmo G., Rees A.P., Denis M., Wang C., Gr egori G., Dong Y., Zhao Y., Zhang W. & Xiao T. 2023. Organization of planktonic Tintinnina assemblages in the Atlantic Ocean. *Frontiers in Marine Science* 10, article no. 1082495, doi: 10.3389/fmars.2023.1082495.
- Li H., Xu Z., Mou W., Gao L., Zu Y., Wang C., Zhao Y., Zhang W. & Xiao T. 2022. Planktonic ciliates in different water masses of Cosmonaut and Cooperation seas (Indian sector of the Southern Ocean) during austral summer. *Polar Biology* 45, 1059–1076, doi: 10.1007/s00300-022-03057-w.
- Li H., Xuan J., Wang C., Chen Z., Gr egori G., Zhao Y. & Zhang W. 2021. Summertime Tintinnid community in the surface waters across the North Pacific Transition Zone. *Frontiers in Microbiology* 12, article no. 697801, doi: 10.3389/fmicb.2021.697801.
- Liang C., Li H., Dong Y., Zhao Y., Tao Z., Li C., Zhang W. & Gr egori G. 2018. Planktonic ciliates in different water masses in open waters near Prydz Bay (East Antarctica) during austral summer, with an emphasis on tintinnid assemblages. *Polar Biology* 41, 2355–2371, doi: 10.1007/s00300-018-2375-5.
- Liang C., Li H., Zhang W., Tao Z. & Zhao Y. 2020. Changes in tintinnid assemblages from Subantarctic Zone to Antarctic Zone along transect in Amundsen Sea (West Antarctica) in early austral autumn. *Journal of Ocean University of China* 19, 339–350, doi: 10.1007/s11802-020-4129-6.
- Marshall J. & Speer K. 2012. Closure of the meridional overturning circulation through Southern Ocean upwelling. *Nature Geoscience* 5, 171–180, doi: 10.1038/ngeo1391.

- Massom R.A., Stammerjohn S.E., Smith R.C., Pook M.J., Iannuzzi R.A., Adams N., Martinson D.G., Vernet M., Fraser W.R., Quetin L.B., Ross R.M., Massom Y. & Krouse H.R. 2006. Extreme anomalous atmospheric circulation in the West Antarctic Peninsula region in austral spring and summer 2001/02, and its profound impact on sea ice and biota. *Journal of Climate* 19, 3544–3571, doi: 10.1175/JCLI3805.1.
- Meredith M.P., Jullion L., Brown P.J., Naveira Garabato A.C. & Couldrey M.P. 2014. Dense waters of the Weddell and Scotia seas: recent changes in properties and circulation. *Philosophical Transactions of the Royal Society A* 372, article no. 20130041, doi: 10.1098/rsta.2013.0041.
- Monti-Birkenmeier M., Diociaiuti T., Castagno P., Budillon G. & Fonda Umani S. 2022. Pluridecadal temporal patterns of tintinnids (Ciliophora, Spirotrichea) in Terra Nova Bay (Ross Sea, Antarctica). *Diversity* 14, article no. 604, doi: 10.3390/d14080604.
- Nöthig E.-M. & Gowing M.M. 1991. Late winter abundance and distribution of phaeodarian radiolarians, other large protozooplankton and copepod nauplii in the Weddell Sea, Antarctica. *Marine Biology* 111, 473–484, doi: 10.1007/BF01319421.
- Park J., Oh I.-S., Kim H.-C. & Yoo S. 2010. Variability of SeaWiFS chlorophyll-a in the southwest Atlantic sector of the Southern Ocean: strong topographic effects and weak seasonality. *Deep-Sea Research Part I* 57, 604–620, doi: 10.1016/j.dsr.2010.01.004.
- Polat S., Terbiyik Kurt T. & Tuğrul S. 2019. Spatial and temporal variations of tintinnids (Ciliata: Protozoa) in the Bay of Mersin, northeastern Mediterranean Sea. *Mediterranean Marine Science* 20, article no. 342, doi: 10.12681/mms.18074.
- Reeve K.A., Boebel O., Strass V., Kanzow T. & Gerdes R. 2019. Horizontal circulation and volume transports in the Weddell Gyre derived from Argo float data. *Progress in Oceanography* 175, 263–283, doi: 10.1016/j.pocean.2019.04.006.
- Rollwagen-Bollens G., Connelly K.A., Bollens S.M., Zimmerman J. & Coker A. 2022. Nutrient control of phytoplankton abundance and biomass, and microplankton assemblage structure in the lower Columbia River (Vancouver, Washington, USA). *Water* 14, article no. 1599, doi: 10.3390/w14101599.
- Santoferrara L.F., Tian M., Alder V.A. & McManus G.B. 2015. Discrimination of closely related species in tintinnid ciliates: new insights on crypticity and polymorphism in the genus *Helicostomella*. *Protist* 166, 78–92, doi: 10.1016/j.protis.2014.11.005.
- Sassi R. & Melo G.D.N. 1986. Tintinnina (Protozoa, Ciliophora, Oligotrichida) from the first Brazilian expedition to the Antarctic. *Anais da Academia Brasileira de Ciências* 58 (Suppl.), 63–83.
- Sitran R., Bergamasco A., Decembrini F. & Guglielmo L. 2007. Temporal succession of tintinnids in the northern Ionian Sea, central Mediterranean. *Journal of Plankton Research* 29, 495–508, doi: 10.1093/plankt/fbm032.
- Smith W.O., Ainley D.G. & Cattaneo-Vietti R. 2007. Trophic interactions within the Ross Sea continental shelf ecosystem. *Philosophical Transactions of the Royal Society B* 362, 95–111, doi: 10.1098/rstb.2006.1956.
- Thoma M., Grosfeld K., Mohrholz C.-O. & Lange M.A. 2005. Modelling ocean circulation and ice–ocean interaction in the southeastern Weddell Sea. *Forum for Research into Ice Shelf Processes (FRISP) Report* 16, 33–42.
- Thompson A.F., Stewart A.L., Spence P. & Heywood K.J. 2018. The Antarctic Slope Current in a changing climate. *Reviews of Geophysics* 56, 741–770, doi: 10.1029/2018RG000624.
- Thompson G. & Alder V. 2005. Patterns in tintinnid species composition and abundance in relation to hydrological conditions of the southwestern Atlantic during austral spring. *Aquatic Microbial Ecology* 40, 85–101, doi: 10.3354/ame040085.
- Trifoglio N.L., Olguín Salinas H.F. & Alder V.A. 2023. Diatoms, tintinnids, and the protist community of the western Weddell Sea in summer: latitudinal distribution and biogeographic boundaries. *Polar Biology* 46, 427–444, doi: 10.1007/s00300-023-03125-9.
- Utermöhl H. 1958. Zur Vervollkommnung der quantitativen Phytoplankton-Methodik. (Methods of collecting plankton for various purposes are discussed.) *Internationale Vereinigung für Theoretische und Angewandte Limnologie: Mitteilungen* 9(1), 1–38, doi: 10.1080/05384680.1958.11904091.
- Vernet M., Geibert W., Hoppema M., Brown P.J., Haas C., Hellmer H.H., Jokat W., Jullion L., Mazloff M., Bakker D.C.E., Brearley J.A., Croot P., Hattermann T., Hauck J., Hillenbrand C.-D., Hoppe C.J.M., Huhn O., Koch B.P., Lechtenfeld O.J., Meredith M.P., Naveira Garabato A.C., Nöthig E.-M., Peeken I., Rutgers van der Loeff M.M., Schmidtko S., Schröder M., Strass V.H., Torres-Valdés S. & Verdy A. 2019. The Weddell Gyre, Southern Ocean: present knowledge and future challenges. *Reviews of Geophysics* 57, 623–708, doi: 10.1029/2018RG000604.
- Wang C., Wang X., Xu Z., Hao Q., Zhao Y., Zhang W. & Xiao T. 2022. Planktonic tintinnid community structure variations in different water masses of the Arctic Basin. *Frontiers in Marine Science* 8, article no. 775653, doi: 10.3389/fmars.2021.775653.
- Wang C., Wang X., Xu Z., Luo G., Chen C., Li H., Liu Y., Li J., He J., Chen H. & Zhang W. 2023. Full-depth vertical distribution of planktonic ciliates (Ciliophora) and a novel bio-index for indicating habitat suitability of tintinnid in the Arctic Ocean. *Marine Environmental Research* 186, article no. 105924, doi: 10.1016/j.marenvres.2023.105924.
- Wang C., Xu Z., Li H., Wang Y. & Zhang W. 2022. Horizontal distribution of tintinnids (Ciliophora) in surface waters of the Ross Sea and polynya in the Amundsen Sea (Antarctica) during summer 2019/2020. *Advances in Polar Science* 33, 28–43, doi: 10.13679/j.advps.2021.0049.
- Williams R., McCall H., Pierce R. & Turner J. 1994. Speciation of the tintinnid genus *Cymatocylis* by morphometric analysis of the loricae. *Marine Ecology Progress Series* 107, 263–272, doi: 10.3354/meps107263.