RESEARCH/REVIEW ARTICLE

Tintinnid ciliates of Amundsen Sea (Antarctica) plankton communities

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Keywords
Zooplankton; microzooplankton; polynya; protists; *Phaeocystis*; diatoms.

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Abstract

The Amundsen Sea has been described as one of the most productive and dynamic pelagic systems in Antarctica and is one of the least studied. Based on samples from 15 stations in the Amundsen Sea, we describe for the first time the composition of the tintinnid ciliate assemblage of the microzooplankton. We compared the species compositions of coastal polynya sites, where the phytoplankton communities are dominated by *Phaeocystis,* to those of the offshore deep water sites, which are dominated by diatoms. We found a total of 15 species. Polynya sites were dominated by a few species of tintinnids, mostly those endemic to the Southern Ocean. In contrast, the deep-water sites contained many widespread tintinnid species, which are known from a wide variety of systems as well as other areas of the Southern Ocean. We examined polymorphism known to characterize the Antarctic tintinnid species *Cymatocylis affinis/convallaria* and *Codonellopsis gaussi*. We found that the types or forms found appeared unrelated to the type of microplankton community, defined by the identity of the dominant phytoplankton taxa. However, the number of different morphotypes found at a site appeared related to the overall concentration of the species, suggesting that different morphologies, previously considered distinct species, may simply be developmental stages.

The Amundsen Sea is a dynamic region of the Antarctic. It was recently described as "one of the most rapidly changing parts of the cyrosphere" (Smith et al. 2011) because it is receiving increasing amounts of meltwater from the West Antarctic Ice Sheet and experiencing winter warming (Ding et al. 2011). Studies based on data from satellite images have concluded that coastal areas of the Amundsen Sea are among the most productive in Antarctica (Arrigo & van Dijken 2003) and that primary production, perhaps fuelled in part by increases in iron input from glacier meltwater, may increase in the future (Arrigo et al. 2012). Paradoxically, the Amundsen Sea is also one of the most poorly sampled areas of the Southern Ocean (Griffiths 2010; De Broyer et al. 2011) and has but recently become a focus of attention in biological oceanography. Primary production in the Amundsen Sea polynya is probably the most productive of any area in Antarctica (Yager et al. 2012). The Amundsen Sea polynya, dominated by the colonial haptophyte *Phaeocystis antarctica*, may increase in relative importance in the future compared to the off-shore communities in which primary production is dominated by large diatoms (Alderkamp et al. 2012).

Tintinnid ciliates are one of the many distinct groups of organisms that make up the marine microzooplankton, the functional group of organisms nominally between 20 and 200 µm in maximal dimension, which are grazers feeding primarily on small phytoplankton sizes ranging from 2 to 20 µm. In most pelagic systems—including different areas of the Southern Ocean (Calbet & Landry 2004)—the microzooplankton are recognized to be the major consumers of primary production, accounting for

Citation: *Polar Research* 2013, *32*, 19784, http://dx.doi.org/10.3402/polar.v32i0.19784

the consumption of about 70% of daily production. Exceptions to this general rule are when primary production is dominated by large diatoms or *Phaeocystis*, as is often the case in productive Southern Ocean waters (e.g., Burkill et al. 1995; Tsuda & Kawaguchi 1997; Caron et al. 2000; Froneman 2004). Compared to oligotrich ciliates or heterotrophic dinoflagellates, tintinnids are generally a minority component of the microzooplankton (e.g., Dolan et al. 1999). However, there are records of tintinnids acting as the dominant consumers of phytoplankton (e.g., Karayanni et al. 2005).

The major predators of tintinnids are usually thought to be copepods although a wide variety of animals are known to consume tintinnids (Stoecker 2012). While there are no data from the Amundsen Sea, in other Southern Ocean systems, gut contents studies have shown that tintinnids are eaten by a variety of both pelagic and benthic organisms. Tintinnid loricae have been found in the guts of crustacean zooplankters such as copepods (Lonsdale et al. 2000; Kruse et al. 2009), krill and mysid shrimp (Mauchline 1980), the zooplankters usually considered the major consumers of microzooplankton (e.g., Froneman et al. 1996). However, other Southern Ocean animals, many not often thought of as predators of microzooplankton, have been found to contain the remains of tintinnids. These include the larger gelatinous zooplankton such as salps (Buck et al. 1992), chaetognaths (Hopkins 1987) and larval Antarctic silverfish (*Pleuragramma antarcticum;* Kellermann 1987). Some benthic organisms of the Antarctic, such as octocorals (Orejas et al. 2003) and deep sea isopods (Brökeland et al. 2010), have been found to contain the remains of tintinnids. In the Southern Ocean, tintinnids appear to be a widely exploited resource.

Unlike the numerically dominant taxa of the microzooplankton, the oligotrichid ciliates and heterotrophic dinoflagellates, tintinnids have species-specific shells or loricae. Hence, species identifications are relatively straightforward, unlike most microplankton taxa. Generally, the tintinnid lorica is tubular or conical but a very large range of constructions is found among the different taxa. The diameter of the open mouth-end of the lorica, the lorica oral diameter (LOD), is an important characteristic not only in terms of taxonomy but it is also a key ecological characteristic. A given species feeds at a maximum rate on prey of a size of about 25% of LOD (Dolan 2010). In common with other protistan taxa with skeletal structures or shells, the characteristics of such hard parts are used to define species despite the fact that some tintinnid species are known to display considerable plasticity in lorica morphology (e.g., Laval-Peuto & Brownlee 1986). Indeed, some Antarctic taxa have long been suspected of showing morphological plasticity. The existence of intermediate forms morphologies described as distinct species led to the suggestion that *Cymatocylis* species may be polymorphic (Boltovskoy et al. 1990; Williams et al. 1994) as well as the species *Codonellopsis gaussi* (Alder 1999). Recent genetic studies have confirmed the suspected polymorphism of *Cymatocylis affinis/convallaria* and *Codonellopsis gaussi* (Kim et al. in press). The factors that may be associated with the different morphologies or forms remain completely unknown.

In late 2010, the maiden voyage of the ice-breaker *Araon* provided the opportunity to make the first direct measurements of primary production in the Amundsen Sea along with analysis of phytoplankton composition (Lee et al. 2012). During the cruise, the stations sampled included both polynya and open-water stations. Material was obtained at 15 stations using a 20-µm plankton net for the analysis of the microplankton community (Fig. 1). To our knowledge, this is the first report on the ecology and species composition of tintinnids of the Amundsen Sea. The only existing data are part of the total ciliate species inventory from the study of Wickham et al. (2011), who provided a species list pooled from several Bellinghausen and Amundsen Sea stations, and the recent study of morphology and phylogeny of selected taxa by Kim et al. (in press). Here, we present data on the composition and distribution of the tintinnid assemblage of the Amundsen Sea. We sought to determine if the tintinnid assemblages found in the non-polynya stations, primarily open deep waters, in which the microplankton community is dominated by diatoms, differed from those found in the coastal polynya stations,

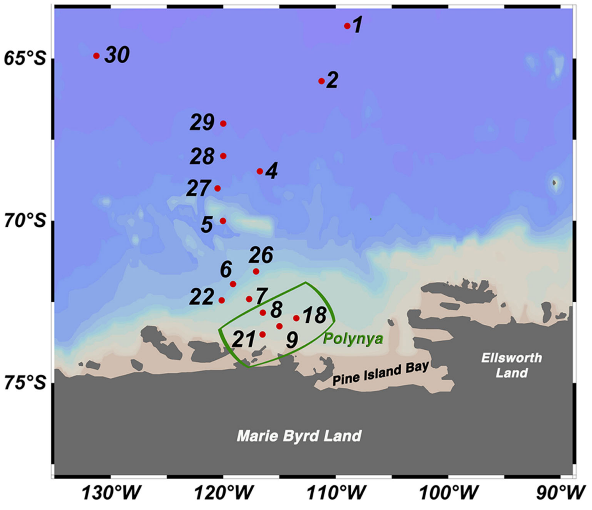

Fig. 1 Location of stations sampled for tintinnids. The green box distinguishes the polynya stations (following Lee et al. 2012).

Citation: *Polar Research* 2013, *32*, 19784, http://dx.doi.org/10.3402/polar.v32i0.19784

dominated by *Phaeocystis*. We also sought to determine if different forms or morphotypes of the polymorphic species *Cymatocylis affinis/convallaria* and *Condonellopsis gaussi* co-occur or are found in different microplankton communities. Here, we use the name *Cymatocylis affinis/convallaria* to remain in conformity with the existing literature (e.g., Boltovskoy et al. 1990; Wasik & Mikolajszyk 1994).

Materials and methods

The data reported were collected during the cruise of the Korean research ice-breaker *Araon* in the Amundsen Sea from December 2010 to January 2011. A Niskin bottle rosette equipped with conductivity—temperature—density probes was used to sample a total of 30 stations and plankton net tows were performed to assess microplankton community composition at 15 of the 30 stations sampled (Fig. 1). Stations were located in both deep offshore waters and polynya areas, considered as coastal areas of open water (free of sea ice) within the sea ice zone; areas of sea ice and concentrations were based on data from the National Snow and Ice Data Center in Boulder, Colorado, corresponding to the cruise period. The classification of stations used here follows that established in Lee et al. (2012).

For chlorophyll *a* determinations, water samples of 0.3–1 L were obtained from 7 to 9 discrete depths between the surface and 150 m depth. Water samples were filtered through a 0.7-µm grade GF/F glass fibre filter (Whatman, Kent, UK) and chlorophyll concentrations were determined on-board using a Trilogy fluorometer (Turner Designs, Sunnyvale, CA, USA) calibrated against commercial chl *a* standards.

Net tows were made with a 20-µm plankton net, 0.45 m in diameter, equipped with a calibrated flowmeter, towed from 150 m depth to the surface. A portion of the net tow material was fixed with Bouin's solution (6% final concentration) for direct microscopic examination. In the laboratory, aliquots of net tow material were sequentially diluted and examined in settling chambers using an inverted microscope equipped with differential interference contrast optics. The entire surface of the settling chamber was examined at 200 × total magnification.

Species identifications were made using the monographs of Kofoid & Campbell (1929, 1939), Hada (1970), Balech (1973) and Alder (1999). Total sample volumes examined varied, depending on the concentrations of tintinnids and the dilutions employed varied according to concentrations of phytoplankton. However, multiple aliquots were examined until at least 50 tintinnids were enumerated for each station (tintinnids enumerated per station ranged from 52 to 358; average 172 ± 139). The sample volumes examined were equal to 1–7 ml of the original 350 ml total net tow material, representing material from about 10–400 L filtered by the net. Nominal concentrations of organisms were calculated based on the apparent volume filtered by the net (as indicated the by net flowmeter) and the volume of net tow material examined. It should be noted that the concentrations reported here are the average values per litre for the top 150 m of the water column. In general, relatively few cells are found below the mixed layer (e.g., Dolan & Marassé 1995). Consequently, the

Table 1 Locations and physical characteristics of the sample stations (see also Fig. 1). Numbers in boldface denote polynya stations and one marginal polynya station (station 8), which was not completely free of sea ice. Station type, mixed layer and euphotic zone depth from, and methods described by Lee et al. (2012).

Station	Lat.	Long.	Date	Depth	Sea ice (%)	Mixed layer depth (m)	Euphotic layer depth (m)
1	63.99	108.99	12/26/10	4990	0	21	45
2	65.69	111.26	12/27/10	4838	0	12	60
4	68.47	116.74	12/28/10	4000	0	13	70
5	70.00	120.02	12/29/10	2900	50–60	13	60
6	71.95	119.13	12/30/10	1451	50–60	18	ND
7	72.41	117.69	12/31/10	530	30–40	15	54
8	**72.83**	**116.48**	**12/31/10**	**640**	**10**	**22**	**ND**
9	**73.25**	**115.00**	**01/01/11**	**1050**	**0**	**54**	**50**
18	**73.00**	**113.50**	**01/06/11**	**448**	**0**	**20**	**20**
21	**73.50**	**116.50**	**01/06/11**	**376**	**0**	**25**	**ND**
22	72.45	120.14	01/07/11	1360	60–70	16	ND
26	71.49	116.95	01/08/11	1364	70–80	22	ND
27	69.00	120.50	01/11/11	1140	0	20	40
28	68.00	120.00	01/11/11	4300	0	12	ND
29	67.00	120.00	01/12/11	4520	0	12	25
30	64.91	131.27	01/13/11	4820	0	14	70

Table 2 Biological characteristics of the stations. The primary production data (^{14}C-based) are from Table 2 in Lee et al. (2012), estimated at a few of the stations sampled for microplankton. Microphytoplankton composition, based on examination of net tow material, was clearly dominated by either diatoms (D), *Phaeocystis* (P) or mixture of both (D/P). Tintinnid concentrations and number of species are shown for the top 150 m of the water column. Values in boldface denote data corresponding to polynya stations or near polynya conditions (station 8).

Station no.	Avg chl (μg l^{-1})[a]	Max chl (μg l^{-1})[b]	Z chl max (m)[c]	Avg PP (μg carbon l^{-1} h^{-1})[d]	Microphyto-plankton	Copepod nauplii	Tintinnids (cells l^{-1})	No. spp.
1	0.4	0.8	40	–	D/P	–	4.9	7
2	0.3	0.5	55	–	D	–	9.8	7
4	0.2	0.3	80	0.009	D	–	5.5	4
5	0.2	0.3	60	0.054	D	–	0.1	4
6	0.3	0.6	35	–	D/P	–	1.3	7
7	0.6	1.8	20	0.327	D	–	3.2	6
8	**1.6**	**5.2**	**15**	**–**	**P**	**0.5**	**2.4**	**4**
9	**5.6**	**11.9**	**10**	**3.500**	**P**	**–**	**–**	**2**
18	**2.5**	**12.2**	**5**	**1.935**	**P**	**1.2**	**5.4**	**4**
21	**4.1**	**11.4**	**5**	**–**	**P**	**0.9**	**7.3**	**4**
22	0.4	1.0	25	–	D/P	–	7.2	5
26	0.2	0.4	30	0.028	D	–	4.3	5
27	0.3	0.4	70	–	D	0.8	1.1	5
28	0.2	0.4	5	–	D	1.9	8.8	4
29	0.3	0.7	10	–	D	0.3	2.6	7
30	0.4	1.1	27	0.176	D	–	6.5	10

[a] Average chlorophyll in integrated throughout the top 150 m of the water column.

[b] The maximum concentration of chlorophyll.

[c] Depth of the chlorophyll maximum.

[d] Primary production integrated throughout the euphotic zone (see Table 1 for euphotic zone depth).

concentrations of cells in the mixed layer were likely several times higher than those reported here, which represent the entire 150 m water column. For several stations, we also enumerated copepod nauplii as a proxy measure of copepod abundance. Simple linear regression was used to investigate the relationships between concentrations (log transformed) of tintinnids and chlorophyll as well as occurrences of different morphotypes.

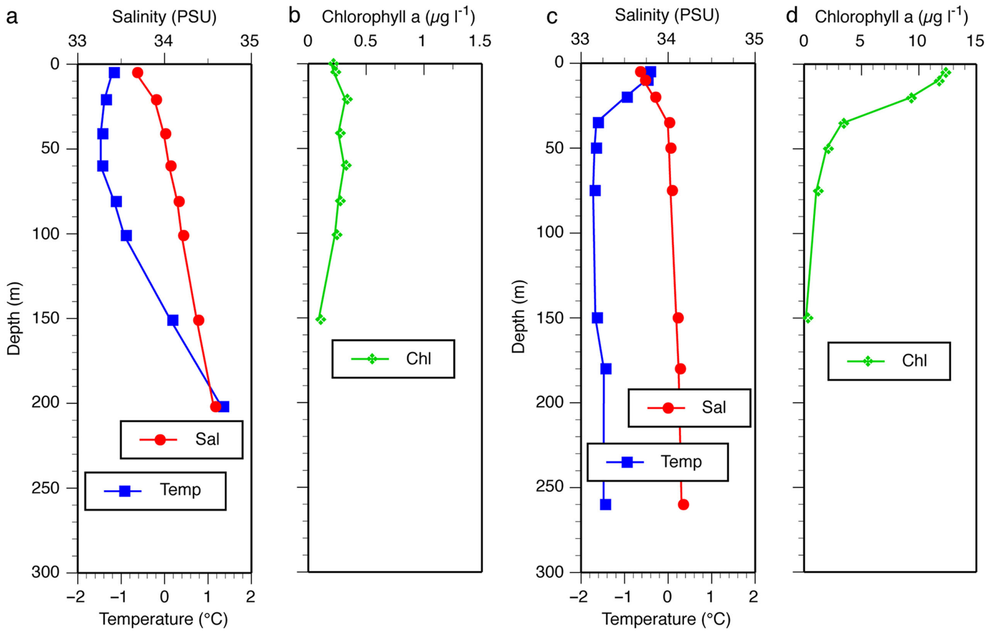

Fig. 2 Water column profiles of (a, b) station 5, typical of deep off-shore stations, and (c, d) a polynya station, station 18. Note the difference in scales of the chlorophyll profiles. For further details see Tables 1 and 2.

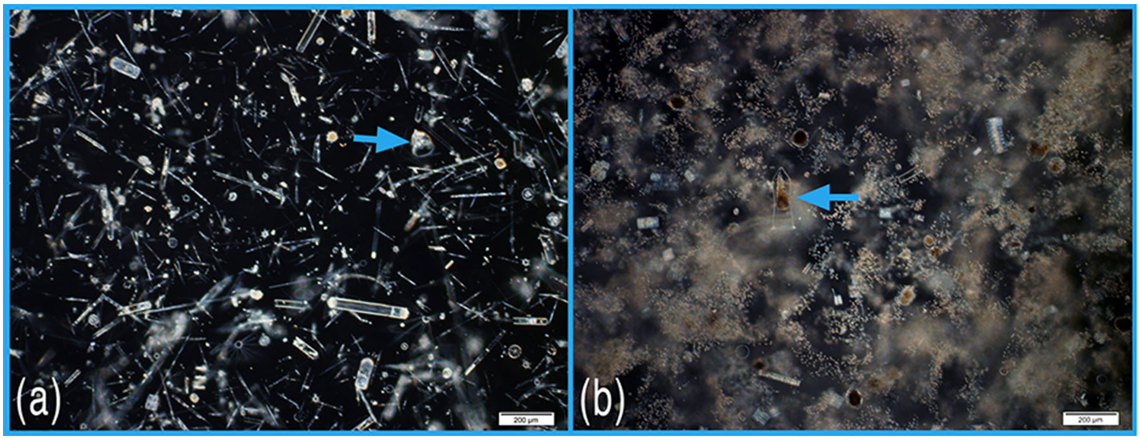

Fig. 3 Low magnification (4 × objective) views of settled net tow material from (a) an offshore deep-water station, station 5, showing a dominance by diatoms, and (b) a coastal polynya station, station 18, showing a dominance by colonies of *Phaeocystis*. The area shown is equivalent to a volume of the original net tow material from about 1 L of seawater. The arrows show tintinnids (*Cymatocylis*).

Results

The physical and biological characteristics of the offshore deep water stations differed considerably from those of the coastal polynya stations. The polynya stations, compared to the non-polynya, primarily offshore sites, were characterized by shallower mixed layer depths (Table 1), considerably higher chlorophyll *a* concentrations with a distinct chlorophyll maximum, and high primary production (Table 2, Fig. 2). The offshore stations were comparatively low in concentrations of chlorophyll and showed more even vertical distributions of chlorophyll. The phytoplankton dominating the microplankton communities was distinctly different also. In the deep water offshore stations, the microplankton was dominated by diatoms while in the polynya stations, microplankton was dominated by *Phaeocystis* (Table 2, Fig. 3). It should be noted that our observations concerning

Table 3 Species records for each station with the station numbers in boldface denoting the polynya stations or near polynya conditions (station 8). The distributional type is based on the biogeographic classifications presented by Dolan et al. (2012). Note that most species were absent from the polynya stations. The species found in polynya were exclusively the Southern Ocean endemic forms except for *Salpingella faurei*. Note that the species *Codondellopsis gaussi* and *Cymatocylis convallaria* group forms previously considered separate species in some reports.

Species	Station occurrence	Distributional type
Acanthostomella obtusa	1, 2	widespread
Amphorellopsis laevis	27	widespread
Amphorellopsis quinqueala	1, 26, 7, 22, 26, 29, 30	Southern Ocean
Amphorides laackmanni	29	widespread
Codonellopsis gaussi	1, 2, 4, 5, 6, 7, **18, 21**, 26, 28, 29, 30	Southern Ocean
Codonellopsis gaussi f. cylindroconica	1, 2, 4, 5, 6, 18, 27, 28, 29, 30	Southern Ocean
Codonellopsis gaussi f. coxiella	6	Southern Ocean
Codonellopsis gaussi f. globosa	30	Southern Ocean
Codondellopsis pusilla	2, 30	widespread
Cymatocylis convallaria f. affinis	1, 2, 5, 6, 7, **8, 9, 18, 21**, 22, 26, 28	Southern Ocean
Cymatocylis convallaria f. calcyformis	1, 2, 26, 30	Southern Ocean
Cymatocylis convallaria f. cylindrica	1	Southern Ocean
Cymatocylis convallaria f. drygalski	1, 2, 5, 6, 7, **8, 9,** 18, **21**, 22, 26, 29	Southern Ocean
Cymatocylis convallaria f. subrotundata	**18**	Southern Ocean
Cymatocylis parva	1, 2, 6	Southern Ocean
Epiplocycloides reticulata	1, 8, 21	widespread
Laackmanniella navaecula	4, 6	Southern Ocean
Laackmanniella prolongata	2, 4, 5, 6, 7, **8, 9, 18, 21**, 22, 26, 27, 28, 29, 30	Southern Ocean
Salpingella curta	6	widespread
Salpingella decurtata	29, 30	widespread
Salpingella faurei	1, 4, 5, 6, 7**, 8, 18, 21**, 22, 26, 27, 28, 29, 30	widespread
Salpingella laackmaniella	7, 22, 27	widespread

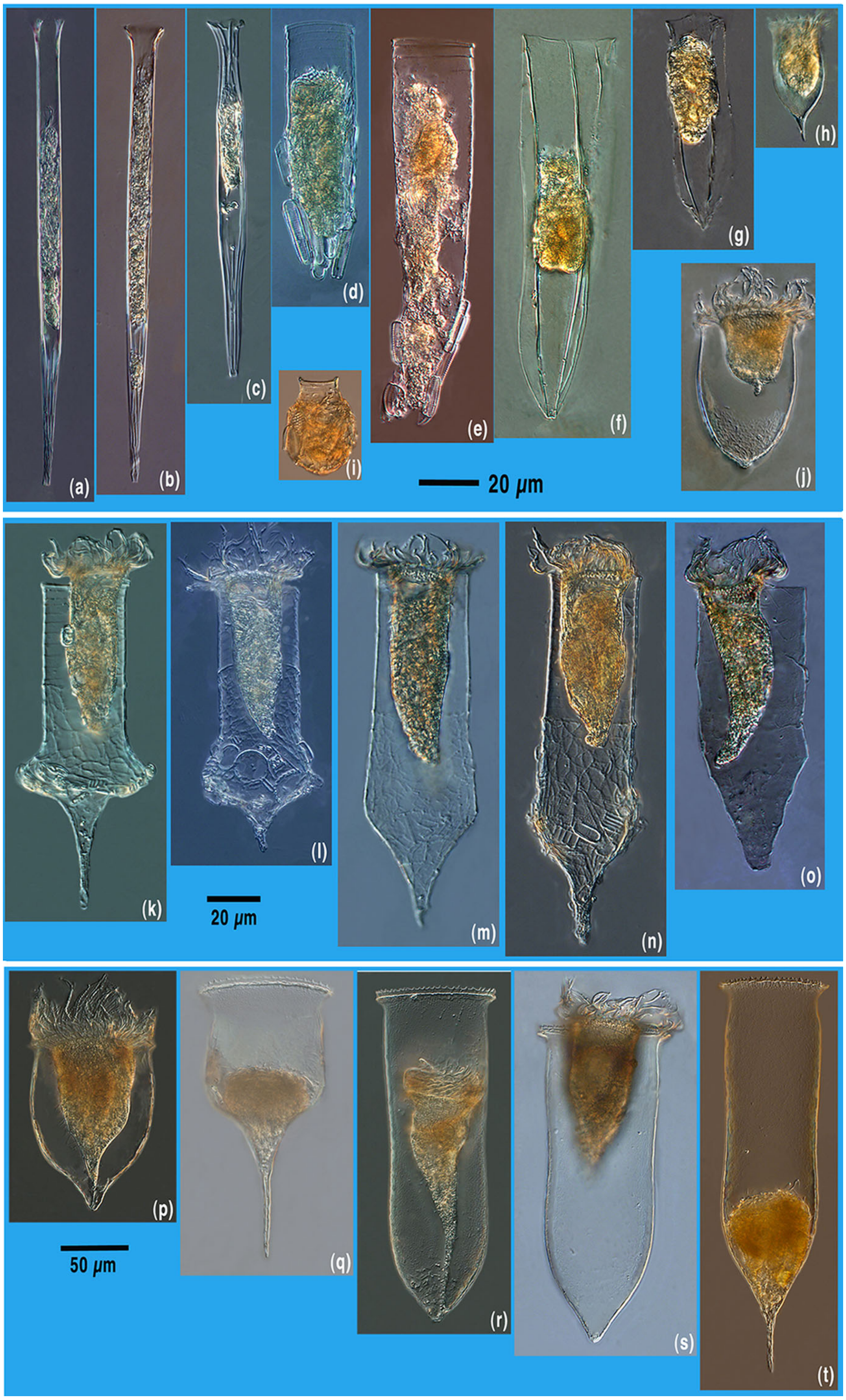

Fig. 4 Tintinnid species encountered in the Amundsen Sea samples. (a) *Salpingella laackmanni*, (b) *Salpingella decurtata*, (c) *Salpingella faurei*, (d) *Laackmanniella naviculaefera*, (e) *Laackmanniella prolongata*, (f) *Amphorellopsis quinquelata*, (g) *Amphorides laackmanni*, (h) *Acanthostomella obtusa*, (i) *Codonellopsis pusilla*, (j) *Epiplocylcoides reticulata*; (k) *Codonellopsis gaussi*, (l) *Codonellopsis gaussi*, (m) *Codonellopsis gaussi* forma *globosa*, (n) *Codonellopsis gaussi* forma *cylindricoconica*, (o) *Condonellopsis gaussi* forma *coxiella*, (p) *Cymatocylis affinis/convallaria*, (q) *Cymatocylis affinis/convallaria* forma *calcyformis*, (r) *Cymatocylis affinis/convallaria* forma *subrotundata*, (s) *Cymatocylis affinis/convallaria* forma *drygalski* and (t) *Cymatocylis affinis/convallaria* forma *cylindrica*. Note that some species agglutinate diatoms; the diatoms are not necessarily the most abundant according to Wasik et al. (1996).

Citation: *Polar Research* 2013, *32*, 19784, http://dx.doi.org/10.3402/polar.v32i0.19784

phytoplankton composition refer to the microplankton community, not the entire phytoplankton community.

A total of 15 species with a wide range of morphologies were encountered in the samples, as well as a variety of morphotypes of two Antarctic species, *Codonellopsis gaussi* and *Cymatocylis affinis/convallaria* (Table 3, Fig. 4). Typically, low species-richness (two to four species) characterized the polynya assemblages compared to the non-polynya assemblages (4–10 species). Furthermore, polynya assemblages were generally dominated by species endemic to the Southern Ocean (largely forms of *Cymatocylis affinis/convallaria* and *Condonellopsis gaussi*) while the offshore assemblages included many widespread tintinnid taxa (Table 3).

Overall, the abundance of tintinnids was clearly not related to bulk chlorophyll concentrations (Table 2). However, plotting chlorophyll data by the dominant type of phytoplankton (diatom, *Phaeocystis*, or both) suggested that within *Phaeocystis*-dominated communities, tintinnid abundance increased with chlorophyll concentrations (Fig. 5). Note that we have no data on the abundance of nano-phytoplankton such as the single-cell forms of *Phaeocystis* or other probable major prey items for tintinnid ciliates.

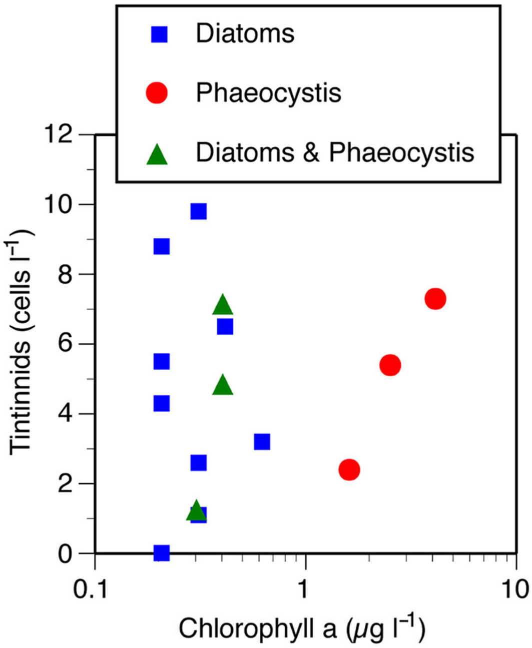

Fig. 5 Scatterplot showing relationship between tintinnid and chlorophyll concentrations in the top 150 m. Symbols distinguish stations in which the microphytoplankton was dominated by diatoms, *Phaeocystis*, or was a mixture of both. There was no significant relationship between tintinnid and overall chlorophyll concentration or among stations in which diatoms dominated the microplankton community. While we have quantitative data for only three of the four polynya stations, the concentration of tintinnids does, however, appear to increase with chlorophyll concentrations in the *Phaeocystis*-dominated communities ($n = 3$, $r = 0.987$).

We found no clear relationship between the composition of the microphytoplankton and the occurrence of different morphologies of *Condonellopsis gaussi* and those of *Cymatocylis affinis/convallaria*. Of the many different "forms," or morphotypes, encountered (Fig. 4), most were found in both the diatom-dominated offshore stations and the *Phaeocystis*-dominated polynya stations (Table 3). There was also no relationship between the number of morphotypes co-occurring and the concentration of chlorophyll, regardless of the identity of the taxa dominating the phytoplankton. However, there was a weak but significant positive relationship between the number of different morphotypes found in an assemblage and the overall concentration of *C. affinis/convallaria* (Fig. 6). There was also a positive trend between the numbers of *C. gaussi* morphotypes or forms found and the overall concentration of *C. gaussi* but not a significant linear relationship.

Discussion

We documented a species-richness for the Amundsen Sea far in excess of that known for the adjacent Bellinghausen Sea (Table 4). There is no doubt that our results reflect the fact that we examined material from large volumes of water sampled with a relatively fine-mesh net. Interestingly, most (nine out of the 15 species) were "widespread" species, found in a variety of systems ranging from the Mediterranean Sea (Dolan 2000) to the Pacific Ocean (Dolan et al. 2007), and all were species which have been previously recorded from other Southern Ocean locations, if not the Bellinghausen Sea (see Dolan et al. 2012). Therefore, none of our species records for the Amundsen Sea are new for the Southern Ocean. However, we did establish for the first time the existence of distinct tintinnid communities in polynya and offshore deep water based on our data concerning the Amundsen Sea.

At the polynya stations, where the microplankton community was dominated by *Phaeocystis*, the tintinnid assemblage was a particular subset of the species catalogue. Only four species were found and three of the four are species endemic to the Southern Ocean: *Cymatocylis affinis/convallaria*, *Codonellopsis gaussi*, *Laackmanniella prolongata*. These Southern Ocean species are all relatively wide-mouth species, with LODs measuring from 40 to 100 µm, presumably feeding most efficiently on prey much larger than those exploited by most of the other species found in the Amundsen Sea (see Fig. 4). While

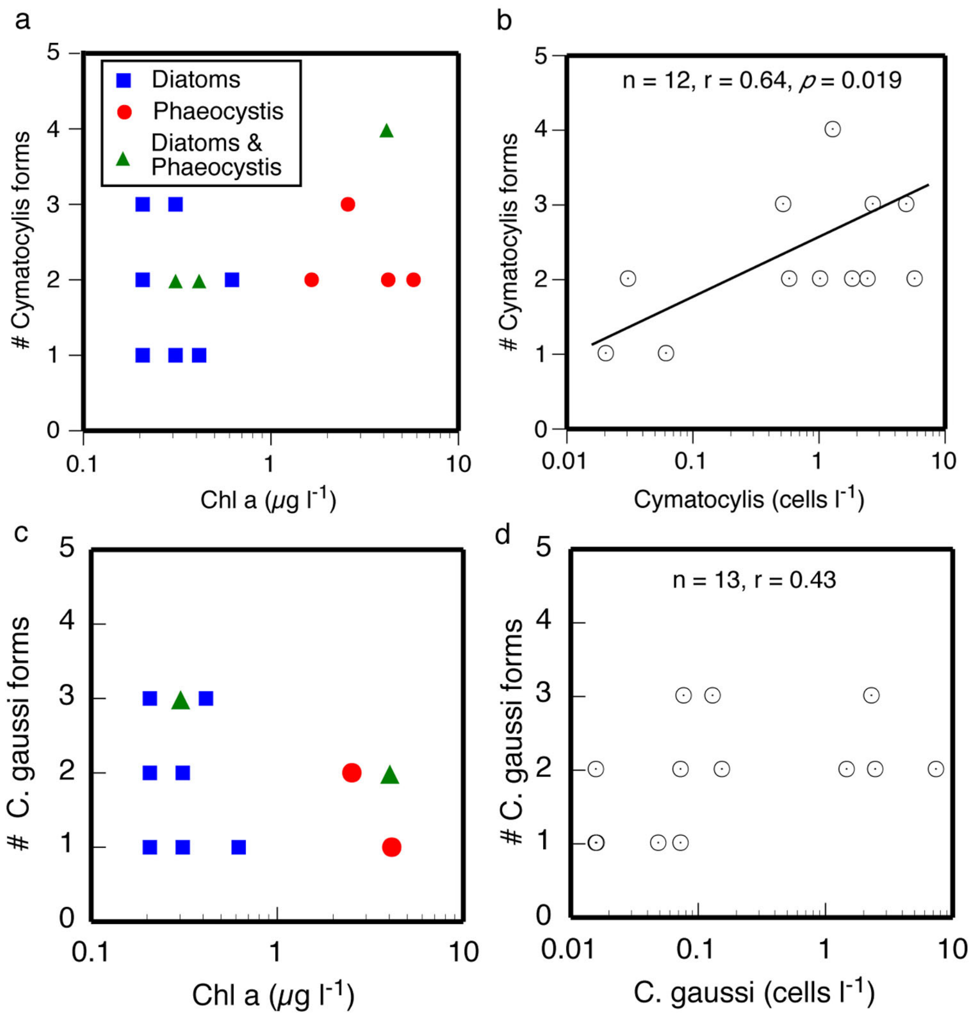

Fig. 6 Scatterplots showing the relationship between the numbers of different forms of (a) *Cymatocylis affinis* and (c) *Condonellopsis gaussi* found in relation to the concentration of chlorophyll (symbols show the dominant phytoplankton forms), and (b, d) the total concentrations of the species, all forms pooled. Note that there is no apparent relationship between numbers of forms and the concentration or composition of the phytoplankton. However, the number of forms found in a station sample was positively related to the overall concentration of *Cymatocylis affinis*, all forms pooled. For *C. gaussi* the relationship was not significant.

there were few data points, it was only among the polynya stations that there appeared to be a relationship between the concentrations of chlorophyll and tintinnids (Fig. 5). However, it is unclear if the relationship could reflect a predator—prey relationship between *Phaeocystis* and tintinnids. Typical planktonic ciliates, such as oligotrichs are unable to graze on colonies of *Phaeocystis* and ingest only the individual free-swimming cells (e.g., Verity 2000). However, tintinnids can reportedly ingest cells from the outer layer of colonies of *Phaeocystis*, crop individual cells, as well as feed on the free-swimming stage (Admiraal & Venekamp 1986). An alternative, but not exclusive, explanation for a positive relationship between *Phaeocystis* concentration and tintinnid abundance is that predation on tintinnids is lower in such communities due to either lower predator abundance or lower predator feeding efficiency with increasing concentrations of *Phaeocystis*. Many polynya areas are known to be characterized by the relatively low abundance of zooplankton (e.g., Tagliabue & Arrigo 2003) and this appears to be the case for Amundsen Sea polynya also (Yager et al. 2012).

We do not have data on the abundance of predators of tintinnids in our polynya compared to non-polynya stations, only some indirect evidence in the form of copepod naupliar concentrations. Our data on copepod nauplii abundance (Table 2) suggests little difference between polynya stations and off-shore stations. However, this is weak evidence of no difference in top—down control of tintinnid composition. Regardless of the

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Table 4 Species records of the Amundsen Sea and the adjacent Bellinghausen Sea. Species names in boldface are endemic to the Southern Ocean; the others are known from a wide range of areas including other regions of the Southern Ocean (Dolan et al. 2012). Species now known to be forms or morphological variants of *Cymatocylis affinis/convallaria* and variants of *Condonellopsis gaussi* (see Table 3) are not listed separately.

Species	Bellinghausen Sea	Amundsen Sea	Bellinghausen/Amundsen
Acanthostomella obtusa		this report	
Amphorellopsis laeva		this report	
Amphorellopsis quinquealata	Balech 1973	Kim et al. in press; this report	
Amphorides laackmanni		this report	Wickham et al. 2011
Codonellopsis balechi	Balech 1973		
Codonellopsis biedermanni			Wickham et al. 2011
Codenellopsis gaussi	Balech 1947, 1973; Alder & Boltovskoy 1991	Kim et al. in press; this report	
Codonellopsis pussila		this report	
Cymatocylis affinis/convallaria	Balech 1947, 1973; Sassi & Melo 1986; Barria de Cao 1987	Kim et al. in press	Wickham et al. 2011
Cymatocylis parva		this report	
Epiplocycloides reticulta		this report	
Helicostomella subulata			Wickham et al. 2011
Laackmanniella naviculaefera	Balech 1973, Sassi & Melo 1986; Barria de Cao 1987; Alder & Boltovskoy 1991	this report	
Laackmanniella prolongata	Balech 1947; Alder & Boltovskoy 1991	Kim et al. in press; this report	
Salpingella curta		this report	
Salpingella decurtata		this report	
Salpingella faurei		this report	
Salpingella laackmaniella		this report	

mechanism influencing tintinnid species composition found in *Phaeocystis*-dominated sites, the projected increase in the relative importance of *Phaeocystis* in the Amundsen Sea (Alderkamp et al. 2012) may be accompanied by increases in the relative importance of the endemic Antarctic species (i.e., *Cymatocylis*, *Laackmaniella*) at the expense of the widespread species found in the diatom-dominated microplankton communities.

We were also interested in examining the phenomenon of polymorphism in the species *Cymatocylis affinis* and *Codonellopsis gaussi* (Fig. 4). Our working hypothesis was that distinct morphologies represent adaptations to distinct conditions. However, we found no evidence that particular morphologies are associated with particular phytoplankton communities. A near full-range of morphologies was found in microplankton communities dominated by diatoms as well as communities dominated by *Phaeocystis* (Table 3). The number of morophotypes found in individual samples was also unrelated to the number of cells enumerated (data not shown). Also, the number of different morphologies found in an assemblage appeared unrelated to the concentration of chlorophyll, regardless of the type of phytoplankton assemblage (Fig. 6a, c).

An alternative explanation for polymorphism is that rather than representing adaptations to a particular environment, the different morphologies found are simply different developmental stages. In this regard, it should be noted that in tintinnids, which reproduce by cell division, the lorica is retained by the newly formed daughter cell, the opisthe, and the cell with the parental mouth, the protor, swims off and forms a new lorica (see Agatha et al. 2012). Consequently, in a population of tintinnids there are both “old” and “new” loricas. The loricas inhabited by many of the tintinnids in a population were formed not by the current inhabitants but rather by ancestral cells and not necessarily direct ancestors but possibly several generations removed.

We speculate that a population of tintinnids, if it is relatively long-lived and experiences rapid bursts of population growth, is liable to contain loricas formed by cells which divided before lorica formation was complete. These partially formed loricas could be retained in the population, inherited by successive generations. Unfortunately, we cannot directly examine this possibility. However, if polymorphism simply reflects different developmental stages, we reasoned that dense populations would exhibit more polymorphism than sparse populations as dense populations are more likely to show characteristics of rapid population growth and thus contain more “immature individuals” corresponding to different morphotypes or forms. We found some evidence in support of the hypothesis as the concentration of *Cymatocylis affinis/convallaria* was positively related to the number of morphotypes in the population (Fig. 6b). A positive (although not significant) trend was also apparent in *Condonellopsis gaussi* (Fig. 6d). Note that these trends were not dependent on the overall number of individuals examined for each station.

Conclusion

We found a high species-richness in the Amundsen Sea compared to the better known adjacent Bellinghausen Sea. We compared, for the first time, the species assemblages of coastal polynya sites, projected to increase in relative importance in the future, with offshore deep water sites. The polynya sites of high primary production dominated by *Phaeocystis*, show a lower species richness and are formed mainly of large-mouthed tintinnid species endemic to the southern Ocean. In the polymorphic species *Cymatocylis affinis/convallaria* and *Codonellopsis gaussi*, the number of types or forms found co-occurring appeared related to the overall concentration of the species, suggesting that the different morphologies may simply be developmental stages.

Acknowledgements

Support for this work was provided by the Korea Polar Research Institute through its PP12010 project as well as by the French National Center for Scientific Research, the University of Paris 6 and the Aquaparadox project, financed by the French National Research Agency programme Biodiversite′ and by Pôle Mer PACA. The thoughtful comments of the reviewers and Steve Wickham are gratefully acknowledged.

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Citation: *Polar Research* 2013, *32*, 19784, http://dx.doi.org/10.3402/polar.v32i0.19784