

Southern Ocean Biogeography of Tintinnid Ciliates of the Marine Plankton

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ABSTRACT. Ciliate microzooplankton are important grazers in most pelagic ecosystems and among them, tintinnids, with their largely species-specific loricas, allow relatively easy assessment of questions of diversity and distributions. Herein, we present the results of a survey of species records of tintinnids from the Southern Ocean (locations below 40°S) reported in 56 publications yielding 2,047 species records (synonyms included) from 402 locations. The 192 species reported can be parsed into two main groups: 32 endemic Southern Ocean species, known only from 40°S and further south, and a second group of 181 widespread species, forms with extensive geographic ranges extending into the Southern Ocean. Widespread species reported from the Southern Ocean can be further divided into a group of 81 species, each recorded multiple times in the Southern Ocean waters and 70 apparent “stray” species which have only been found but once. The endemic and widespread species of the Southern Ocean show both distinct distributional patterns and morphological differences. The assemblage of Southern Ocean endemics is found mostly within the Antarctic zone delimited by the average location of the Polar Front and contains a relatively large portion of wide-mouthed forms. We give suggestions for future study.

Key Words. Antarctica, endemism, microzooplankton, sea ice, zooplankton.

GENERAL CHARACTERISTICS OF TINTINNIDS AND ECOLOGICAL ROLE IN THE SOUTHERN OCEAN

TINTINNIDS are planktonic ciliate protists found in the surface layer waters of nearly all marine and estuarine systems. The suborder Tintinninea is a very speciose taxon; the standard taxonomic monographs of Kofoid and Campbell (1929, 1939) catalog over 700 species and usually many species are found coexisting. For example, a single sampling in the NW Mediterranean revealed 34 species (Dolan and Stoeck 2011). Large-scale biogeographic patterns are well-known. Tintinnids literally supply a textbook example of the latitudinal species gradient (e.g. Gaston and Spicer 2003). Most genera can be characterized as predominately found in either coastal or open waters and as temperate, tropical, or high latitude fauna (e.g. Pierce and Turner 1993). Using Pierce and Turner's terminology, some genera are “boreal,” known only from Arctic and Subarctic zones (i.e. *Parafavella* and *Ptychocylis*), and others are “austral,” found only in Antarctic or Subantarctic waters (i.e. *Cymatocylis* and *Laackmanniella*), herein, considered together as the Southern Ocean. Nonetheless, some tintinnid species appear to be cosmopolitan as they are found in all oceanographic biomes, sensu Longhurst (1998). A recent review described very similar broad-scale patterns of global distribution among aloricate oligotrich taxa with some taxa apparently cosmopolitan and others endemic to certain biomes, such as the Antarctic, the North Pacific or the Black Sea (Agatha 2011). It is perhaps worth noting that in recent years rather than “everything is everywhere,” the view that varying degrees of endemism characterizes most protist groups has become the dominant school of thought (e.g. Fontaneto and Brodie 2011).

In terms of a functional group, tintinnid ciliates are part of the microzooplankton, that is grazers nominally between 20 and 200 microns in maximal dimension feeding primarily on

small phytoplankton of cell sizes ranging from 2 to 20 μm . Microzooplankton are acknowledged to be the major consumers of primary production in the most planktonic systems (Calbet and Landry 2004). This is also true of different areas of the Southern Ocean, but only when primary production is not dominated by large diatoms or *Phaeocystis* (e.g. Burkill et al. 1995; Caron et al. 2000; Froneman 2004; Tsuda and Kawaguchi 1997). Occasionally, the feeding activity of tintinnids can dominate the consumption of phytoplankton (e.g. Karayanni et al. 2005), but they are generally a minority component of the microzooplankton compared with other protists of the microzooplankton, such as oligotrich ciliates or heterotrophic dinoflagellates. In tintinnids, gape size, in the form of the diameter of the mouth-end of the lorica, the lorica oral diameter (LOD), is related to the size of the food items ingested. The largest prey ingested is commonly about half the LOD in longest dimension (Heinbokel 1978), and they feed most efficiently, removing prey at maximum rates, on prey about 25% of LOD in size (Dolan 2010). The overwhelming majority of described species have an LOD between 20 and 60 μm indicating a typical prey size range of 5–15 μm . Tintinnids serve as prey for a large number of pelagic organisms in the Southern Ocean, such as copepods, krill, and mysid shrimp, larger organisms, such as salps, chaetognaths, and larval Antarctic silverfish as well as benthic organisms, such as octocorals and deep-sea isopods (Brökeland et al. 2010; Buck et al. 1992; Hopkins 1987; Kellermann 1987; Kruse et al. 2009; Lonsdale et al. 2000; Mauchline 1980; Orejas et al. 2003).

Species identifications of tintinnids are based on characteristics of the lorica into which the ciliate cell can withdraw. The general shape of the lorica (or shell) of a tintinnid is a tube or vase shape, but a very large range of lorica architecture is shown by different forms, including those typical of the Southern Ocean (e.g. Fig. 1). Like other groups of planktonic protists, such as foraminifera and radiolarians, characteristics of gross morphology define species, although some species are known to display considerably plasticity in lorica morphology (e.g. Laval-Peuto and Brownlee 1986). Tintinnids, in contrast with other groups of planktonic ciliates, for example, “oligotrichs,” are, but a single order even among competing ciliate classification schemes. According to traditional ciliate taxonomy, and in agreement with recent molecular studies (Agatha

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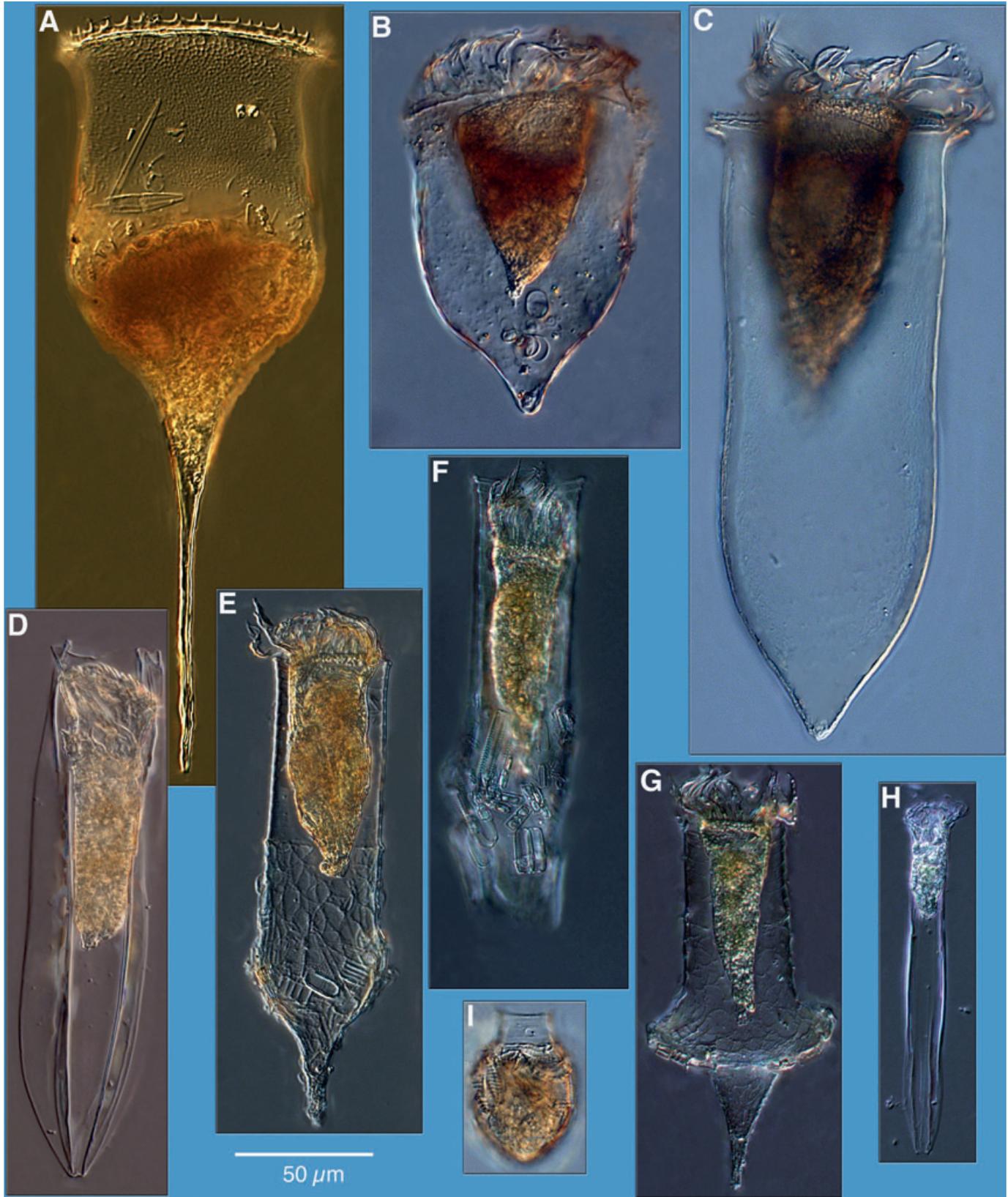


Fig. 1. Examples of tintinnid species or morphotypes commonly reported from the Southern Ocean. All are Bouin's-fixed specimens from the Amundsen Sea. (A) *Cymatoecylis calcyformis*, (B) *Cymatoecylis convallaria-affinis*, (C) *Cymatoecylis drygalski*, (D) *Amphorellopsis quinquealata*, (E) *Condonellopsis gaussi* f. *cylindrica*, (F) *Laackmanniella prolongata*, (G) *Condonellopsis gaussi*, (H) *Salpingella faurei*, (I) *Condonellopsis pusilla*. All but *Salpingella faurei* and *Condonellopsis pusilla* are forms found only in the Southern Ocean.

and Strüder-Kype 2012; Bachy et al. 2012; Saccà et al. 2012; Santoferrara et al. 2012a,b), they are a monophyletic group. Thus, tintinnids are a coherent group ecologically as microzooplankton, morphologically as loricate ciliates, and phylogenetically as members of the order Tintinnida.

There have been no surveys nor synoptic studies of tintinnids in the Southern Ocean or in Antarctic waters. Species occurrence and distributions can only be assessed by synthesizing the many individual reports mostly concerning a single or a few locations. Herein we describe patterns that emerge from a database of tintinnid species occurrence compiled from such reports in the literature. We consider the Southern Ocean to be the global zone between 40 and 78°S. For a pertinent, concise review of the physical and biological characteristics of the zone see Griffiths (2010) from which our definitions and locations of the Polar Front and extent of winter-time ice coverage are drawn. For an engaging account of the history of studies of the “Antarctic Circumpolar Ocean” see Deacon (1984).

The original database was previously described and used to establish global patterns at the genus level (Pierce and Turner 1993). For Southern Ocean locations, the original database consisted of species names, latitude, longitude, and year of report from 23 publications containing 1,150 Southern Ocean species records. It was updated to include post-1992 publications, the year of actual sampling for each species record, and revised to account for current taxonomy. The updated database consisted of 2,047 species records (synonyms included) from 56 publications reporting on species found in 402 locations. The literature reports consulted are given in Table S1.

It should be noted that we use the term “species” in our descriptions of distributional patterns, but the term could be replaced by the more accurate term “morpho-species.” In ciliates, the relationship between morpho-species and the generally accepted biological definition of “species” remains unclear because morphology, mating types, and genetics can be discordant (Hall and Katz 2011). For tintinnids, the limited genetic data available suggest morpho-species of tintinnids, rather than grouping cryptic species (forms morphologically similar, but genetically distinct), may more often be different phenotypes of the same genetic species. First, it appears that geographically distant populations of planktonic ciliates can be genetically identical (Agatha et al. 2004; Katz et al. 2005). Thus, there is a priori no reason to associate geographic separation in species of planktonic ciliates with genetic isolation. Secondly, while genetic studies of tintinnids have only recently begun, identical or nearly identical small subunit RNA sequences have been found for distinctly different morphologically defined species’ of *Tintinnopsis* (Li et al. 2009), *Favella* (Kim et al. 2010), *Petalotrichia/Cyttarocylis* (Bachy et al. 2012), *Cymatocylis*, and *Laackmanniella/Codonellopsis* (Kim S. Y., Choi J. K., Dolan J. R., Shin H. C., Lee S.-H. & Yang E. J., unpubl. data). Furthermore, thus far no truly cryptic species have been discovered among tintinnids. However, there is a recent report of two forms of *Helicostomella*, genetically distinct, but largely overlapping in morphological characteristics (Xu et al. 2012).

Overall, there are records for 192 currently recognized species of tintinnids from locations below 40°S, based on reports published from 1900 to 2011. Mapping the data shows that sites sampled to date are distributed very irregularly in the Southern Ocean (Fig. 2.). The area between the South Atlantic and the Weddell Sea has provided a disproportionately large number of samples. Large areas of the Southern Ocean have received little attention and we can only speculate as to whether or not the well-sampled areas are representative or not. The temporal distribution of sampling effort has also been irregularly distributed over the past 112 yr (Fig. 3). Not

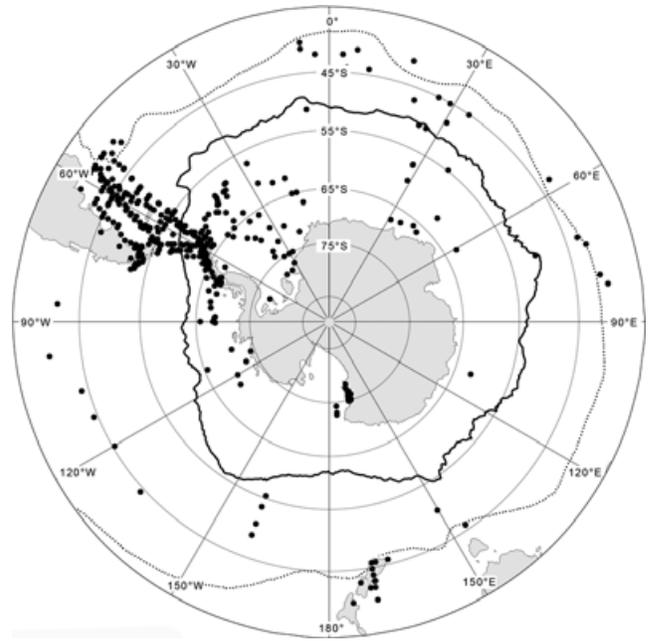


Fig. 2. Locations of sites from tintinnids have been reported from Southern Ocean sites. The heavy line in the Southern Ocean map denotes the average location of the Polar Front and the dotted line the average location of the subtropical front (the northern limit of the Southern Ocean), based on Griffiths (2010). Please see Table S1.

surprisingly, nearly all the sampling has been performed during the summer months of the Southern Hemisphere. The majority of species records are based on examination of plankton net material often with no data given on the volumes of water nominally sampled nor the mesh-size. Therefore, the data are qualitative only.

HISTORICAL PERSPECTIVE

To our knowledge, the first report of tintinnids from the Southern Ocean is that of Cleve who reported on a variety of planktonic organisms (Cleve 1900). Interestingly, he also noted that some forms, (not only tintinnids, but also diatoms and dinoflagellates of the phytoplankton) found in the Southern Ocean are also typical of northern temperate or Arctic waters, whereas still others appeared to be “characteristic of the Antarctic region.” Although his was not the first notation of the existence of apparently “bi-polar” species in the plankton, he was the first to describe a tintinnid, *Acanthostomella norvegica*, as such. Cleve believed his findings led support to Carl Chun’s speculations on the existence of deep-sea currents linking Arctic and Antarctic waters. However, it should be noted in passing that in protists other than tintinnids “cryptic species” are common with Arctic and Antarctic populations genetically distinct (e.g. Darling et al. 2007).

The first focused studies of Southern Ocean tintinnids date back to material gathered during the German South Polar expedition of 1901–1903. On the basis of the samples gathered, Hans Laackmann first briefly described a few new species of tintinnids (Laackmann 1907) and subsequently produced a monographic study, describing a large number of new species and varieties (Laackmann 1910). He was the first to note that the species “characteristic of the Antarctic,” *Cymatocylis* and species now known as *Laackmanniella*, had

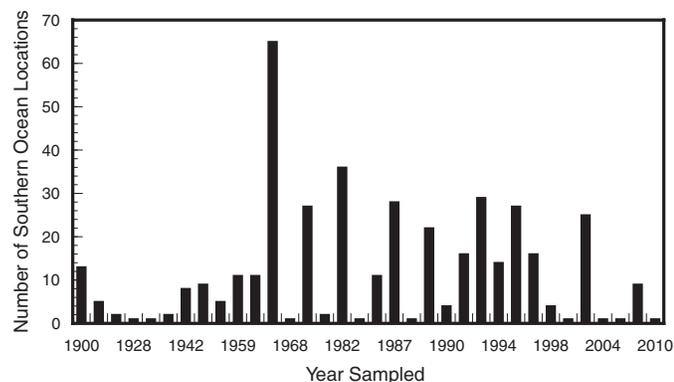


Fig. 3. Temporal distribution of sampling effort in Southern Ocean from studies, which reported data on tintinnid species occurrences.

close correspondence or similarity in general morphologies with the species typical of Arctic waters, *Ptychocylis*, *Parafavella*, and *Leprotintinnus*.

Relatively few locations were sampled in the Southern Ocean throughout the first half of the 20th century (Fig. 3). The large number of sites sampled in the 1960s and 1970s is mostly from the studies of Enrique Balech describing material gathered by Argentine expeditions between the South Atlantic and Weddell Sea. The most recent reports furnishing data on Southern Ocean tintinnids are the study of Fonda Umami et al. (2011), which focused on sites from the Straits of Magellan, and Wickham et al. (2011).

GEOGRAPHIC DISTRIBUTIONS OF SOUTHERN OCEAN TINTINNID SPECIES

The 192 species reported from locations between 40 and 78°S can be parsed into two main groups: Southern Ocean species, those known only from 40°S and further south, and a second group of widespread species, those whose extensive geographic ranges extend into the Southern Ocean. Tintinnid species restricted to the Southern Ocean comprise a group of 32 species, which have not been reliably reported north of 40°S (Table 1). The figure of 32 accounts for recent findings of synonymy (Kim S. Y., Choi J. K., Dolan J. R., Shin H. C., Lee S.-H. & Yang E. J., unpubl. data) with regard to several species: four species of *Cymatocylis* (*C. affinis* = *C. calcyformis*, *C. convallaria*, & *C. drygalski*), two species of *Condonellopsis* (*C. gaussi* & *C. glacialis* = *Laackmanniella*), and two species of *Laackmanniella* (*L. prolongata* = *L. naviculaefera*). The spatial distributions of two genera with the largest number of recorded occurrences, *Cymatocylis*, and *Laackmanniella* are shown in Fig. 4, 5. Although both genera appear to be largely restricted to waters within the Polar Front, *Cymatocylis* has been found much more frequently outside the area occupied by sea ice during the Southern Ocean winter compared with *Laackmanniella*, which appears then to be more exclusively “Antarctic” than *Cymatocylis*.

The second group of widespread species is comprised of 161 taxa found in not only in the Southern Ocean, but elsewhere as well. This very large set of species can be divided into two sets: the 81 species, which have been recorded multiple times in the Southern Ocean waters (Table 2), and the 70 species, which have only been found once below 40°S (Table 3). The latter set of species with, but a single Southern Ocean record can be considered as a list of “strays” as not only are the species rare in the Southern Ocean, as evidenced by the single report, but

Table 1. Southern Ocean species

Southern Ocean endemic species	# records	Lat min	Lat max
<i>Amphorellopsis quinquealata</i>	13	58	68
<i>Codonellopsis antarctica</i>	6	48	62
<i>Codonellopsis balechi</i>	38	49	78
<i>Cymatocylis affinis-conval-calcy-drygal</i>	146	50	78
<i>Cymatocylis antarctica</i>	90	45	65
<i>Cymatocylis brevicaudata</i>	5	51	62
<i>Cymatocylis cristallina</i>	2	59	60
<i>Cymatocylis cristallina</i>	3	60	74
<i>Cymatocylis culcullus</i>	2	59	66
<i>Cymatocylis cylindroides</i>	2	59	60
<i>Cymatocylis cylindrus</i>	3	60	62
<i>Cymatocylis ecaudata</i>	4	60	75
<i>Cymatocylis flava</i>	16	59	78
<i>Cymatocylis folliculus</i>	4	60	75
<i>Cymatocylis glans</i>	2	66	75
<i>Cymatocylis kerguelensis</i>	2	49	55
<i>Cymatocylis incondita</i>	1	69	69
<i>Cymatocylis nobilis</i>	8	58	75
<i>Cymatocylis ovata</i>	5	60	65
<i>Cymatocylis parva</i>	6	56	66
<i>Cymatocylis scyphus</i>	2	59	60
<i>Cymatocylis subconica</i>	3	66	75
<i>Cymatocylis subrotundata</i>	8	65	75
<i>Cymatocylis typica</i>	5	59	62
<i>Cymatocylis vanhoeffeni</i>	40	47	77
<i>Cyrtarocylis conica</i>	3	60	62
<i>Daturella frigida</i>	1	62	62
<i>Eutintinnus subrugosa</i>	1	58	58
<i>Laackmanniella</i>	127	43	78
<i>Helicostomella lemairei</i>	2	56	58
<i>Steenstrupiella pozzi</i>	92	40	61
<i>Tintinnopsis bacillaria</i>	13	41	64

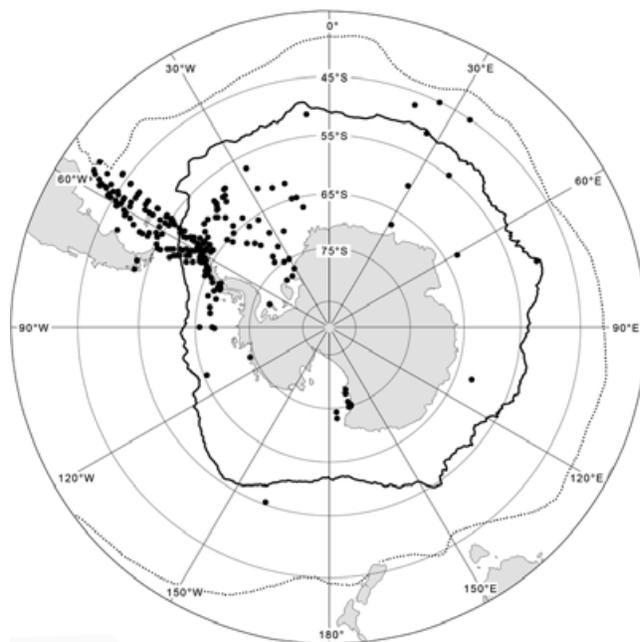


Fig. 4. Location of sites from which *Cymatocylis* spp. have been reported. The heavy line in the Southern Ocean map denotes the average location of the Polar Front and the dotted line the average location of the subtropical front (the northern limit of the Southern Ocean).

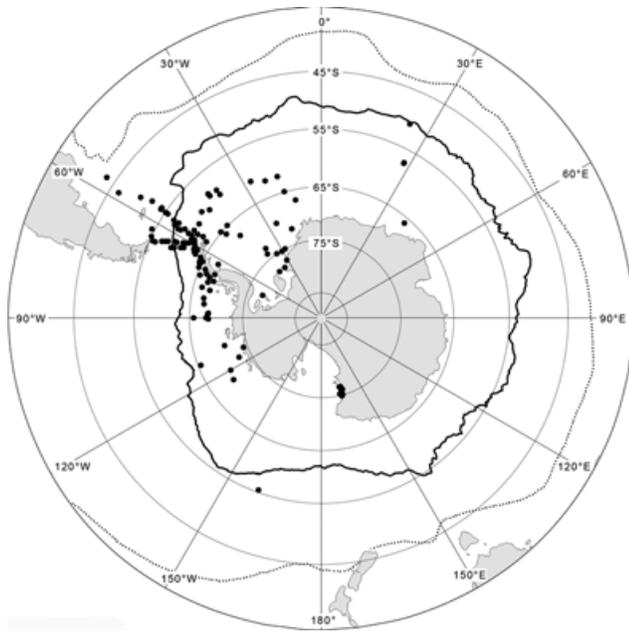


Fig. 5. Location of sites from which *Laackmanniella* spp. have been reported. The heavy line in the Southern Ocean map denotes the average location of the Polar Front and the dotted line the average location of the subtropical front (the northern limit of the Southern Ocean).

none has been reported to occur in significant abundance. In contrast, many of the widespread species reported multiple times appear to be very common in tintinnid assemblages in the Southern Ocean. For example, *Codonellopsis pusilla* has been recorded nearly as often as the Southern Ocean species of *Cymatocylis* and *Laackmanniella*. The ubiquity or rarity of a species in the records from the Southern Ocean appears unrelated to whether or not the species is a Southern Ocean species. The number of records for each of 192 species ranked according to “ubiquity”—their relative frequency of occurrence in the sites sampled, is shown in Fig. 6. Widespread species, those found outside as well as inside the Southern Ocean, rank within the 10 most commonly reported species in records from the Southern Ocean. Nonetheless, examination of a map showing sites sampled in the Southern Ocean from which only endemic species were reported, thus apparently less inhabited by widespread species, shows a concentration of such sites inside the zone delimited by the extent of the Polar Front (Fig. 7). Conversely, sites from which only widespread species were recorded are concentrated at the northern edge of the Southern Ocean (Fig. 8). A very similar apparent dichotomy in distribution between endemic and widespread diatoms in the Southern Ocean has been reported (Armand et al. 2005; Crosta et al. 2005; Romero et al. 2005). With regard to the endemic tintinnid species, while we cannot identify the characteristics defining the zone which favor their development, the zone appears to be a better predictor of Antarctic tintinnid occurrence than the northern limit of the Southern Ocean.

MORPHOLOGICAL CHARACTERISTICS OF SOUTHERN OCEAN TINTINNIDS

The average LOD of tintinnid assemblages can differ considerably between systems and is thought to reflect the size spectrum of food items exploited (Dolan et al. 2009). Conse-

Table 2. Widespread species with multiple southern Ocean records.

<i>Acanthostomella lata</i>	<i>Eutintinnus fraknoi</i>	<i>Salpingella subconica</i>
<i>Acanthostomella norvegica</i>	<i>Eutintinnus lusus-undae</i>	<i>Steenstrupiella intumescens</i>
<i>Amphorellopsis acantharus</i>	<i>Eutintinnus medius</i>	<i>Steenstrupiella steenstrupii</i>
<i>Amphorides amphora</i>	<i>Eutintinnus rectus</i>	<i>Stenosemella avellana</i>
<i>Amphorides brandti</i>	<i>Eutintinnus tubulosus</i>	<i>Stenosemella nivalis</i>
<i>Amphorides laackmanni</i>	<i>Helicostomella subulata</i>	<i>Stenosemella ventricosa</i>
<i>Amphorides quadrilineata</i>	<i>Luminella (Stenosemella) pacifica</i>	<i>Stylicauda platensis</i>
<i>Ascampbelliella acuta</i>	<i>Ormosella haeckeli</i>	<i>Tintinnopsis baltica</i>
<i>Ascampbelliella armilla</i>	<i>Parundella aculeata</i>	<i>Tintinnopsis beroidea</i>
<i>Ascampbelliella protuberans</i>	<i>Parundella caudata</i>	<i>Tintinnopsis cylindrica</i>
<i>Ascampbelliella urceolata</i>	<i>Parundella crassicaudata</i>	<i>Tintinnopsis gracilis</i>
<i>Bursaopsis ollula</i>	<i>Parundella pellucida</i>	<i>Tintinnopsis karajacensis</i>
<i>Codonella amphorella</i>	<i>Poroecus curtus</i>	<i>Tintinnopsis lata</i>
<i>Codonella aspera</i>	<i>Proplectella claparedei</i>	<i>Tintinnopsis levigata</i>
<i>Codonella elongata</i>	<i>Proplectella fastigata</i>	<i>Tintinnopsis lobiancoi</i>
<i>Codonellopsis morchella</i>	<i>Proplectella globosa</i>	<i>Tintinnopsis major</i>
<i>Codonellopsis pusilla</i>	<i>Proplectella subacuta</i>	<i>Tintinnopsis meunieri</i>
<i>Codonellopsis schabi</i>	<i>Proplectella subcaudata</i>	<i>Tintinnopsis minuta</i>
<i>Dadayiella ganymedes</i>	<i>Protocymatocylis pseudiconica</i>	<i>Tintinnopsis nucula</i>
<i>Dietyocysta californiensis</i>	<i>Protorhabdonella curta</i>	<i>Tintinnopsis parva</i>
<i>Dietyocysta duplex</i>	<i>Protorhabdonella simplex</i>	<i>Tintinnopsis parvula</i>
<i>Dietyocysta elegans</i>	<i>Rhabdonella amor</i>	<i>Tintinnopsis rapa</i>
<i>Dietyocysta fenestrata</i>	<i>Rhabdonella chilensis</i>	<i>Tintinnopsis sacculus</i>
<i>Dietyocysta lepida</i>	<i>Rhabdonella indica</i>	<i>Tintinnopsis turbo</i>
<i>Dietyocysta mitra</i>	<i>Rhabdonella spiralis</i>	<i>Tintinnopsis vasculum</i>
<i>Dietyocysta reticulata</i>	<i>Salpingella acuminata</i>	<i>Xystonella acus</i>
<i>Dietyocysta speciosa</i>	<i>Salpingella decurtata</i>	<i>Xystonella lanceolata</i>
<i>Epiplocylis acuminata</i>	<i>Salpingella faurei</i>	<i>Xystonella longicauda</i>
<i>Epiplocylis undella</i>	<i>Salpingella glockentögeri</i>	
<i>Eutintinnus apertus</i>	<i>Salpingella laackmanni</i>	

quently, it is of interest to consider this characteristic in comparing tintinnid populations. The species pool of Southern Ocean tintinnids, excluding species recorded but once (strays and questionable species), numbers 120. This large number of species includes a very wide range of lorica oral diameters, approximately as wide as the global tintinnid species catalog and a frequency distribution similar with that of global species catalog of about 700 species (Fig. 9). The only apparent difference is that the species assemblage of the Southern

Table 3. Widespread species with a single Southern Ocean record.

<i>Acanthostomella conicoides</i>	<i>Favella azorica</i>
<i>Acanthostomella minutissima</i>	<i>Favella campanula</i>
<i>Acanthostomella obtusa</i>	<i>Favella taraiakaensis</i>
<i>Amphorellopsis acuta</i>	<i>Leprotintinnus nordquisti</i>
<i>Amphorellopsis laevis</i>	<i>Metacyclis annulifera</i>
<i>Amplectella monocollaria</i>	<i>Metacyclis corbula</i>
<i>Ascampbelliella aperta</i>	<i>Parafavella brandti</i>
<i>Climacocyclus scalaria</i>	<i>Parundella messinensis</i>
<i>Climacocyclus scalaroides</i>	<i>Petalotricha ampulla</i>
<i>Codonellopsis biedermanni</i>	<i>Petalotricha pacifica</i>
<i>Codonellopsis brevicaudata</i>	<i>Proplectella perpusilla</i>
<i>Codonellopsis contracta</i>	<i>Rhabdonella brandti</i>
<i>Codonellopsis indica</i>	<i>Rhabdonella cornucopia</i>
<i>Codonellopsis ostenfeldi</i>	<i>Rhabdonella quantula</i>
<i>Codonellopsis parvicollis</i>	<i>Rhabdonellopsis apophysata</i>
<i>Cymatocyclus conica</i>	<i>Rhabdonellopsis intermedia</i>
<i>Cymatocyclus subconica</i>	<i>Salpingella acuminatoides</i>
<i>Daturella luanae</i>	<i>Salpingella secata</i>
<i>Dictyocysta obtusa</i>	<i>Salpingella undata</i>
<i>Dictyocysta polygonata</i>	<i>Steenstrupiella gracilis</i>
<i>Epiplocyloides acuta</i>	<i>Tintinnopsis brasiliensis</i>
<i>Epiplocyloides ralumensis</i>	<i>Tintinnopsis bütschlii</i>
<i>Epiplocyclus blanda</i>	<i>Tintinnopsis compressa</i>
<i>Epiplocyclus constricta</i>	<i>Tintinnopsis glans</i>
<i>Epiplocyclus deflexa</i>	<i>Tintinnopsis radix</i>
<i>Epiplocyclus exigua</i>	<i>Tintinnopsis rotundata</i>
<i>Epiplocyclus healdi</i>	<i>Tintinnopsis tocaninensis</i>
<i>Epiplocyclus inflata</i>	<i>Tintinnopsis tubulosa</i>
<i>Epiplocyclus lata</i>	<i>Tintinnopsis urnula</i>
<i>Epiplocyclus mira</i>	<i>Undella declivis</i>
<i>Eutintinnus attenuatus</i>	<i>Undella hemispherica</i>
<i>Eutintinnus australis</i>	<i>Undella parva</i>
<i>Eutintinnus elegans</i>	<i>Undella turgida</i>
<i>Eutintinnus pacificus</i>	<i>Xystonella trefortii</i>
<i>Eutintinnus pinguis</i>	
<i>Eutintinnus stramentus</i>	

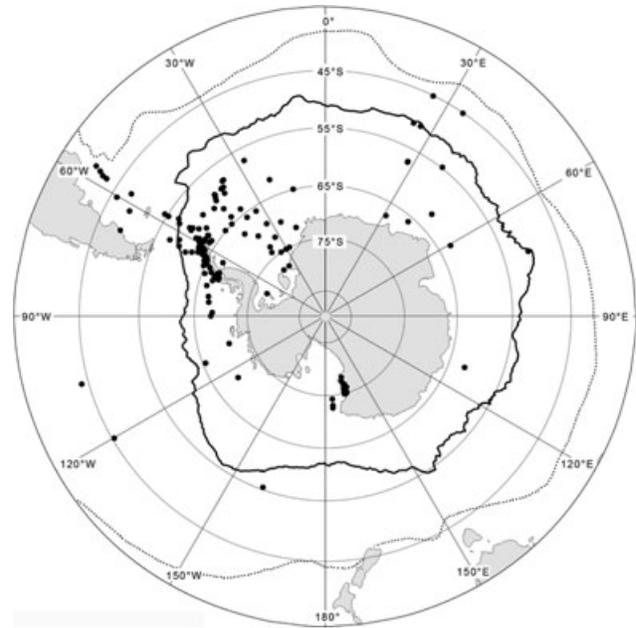


Fig. 7. Locations from which only endemic species were reported. Out of the 402 Southern Ocean sites sampled, from 151 sites only endemic species were reported. These sites, at which no widespread species were reported, are mostly within the area defined by the Polar Front (the bold line).

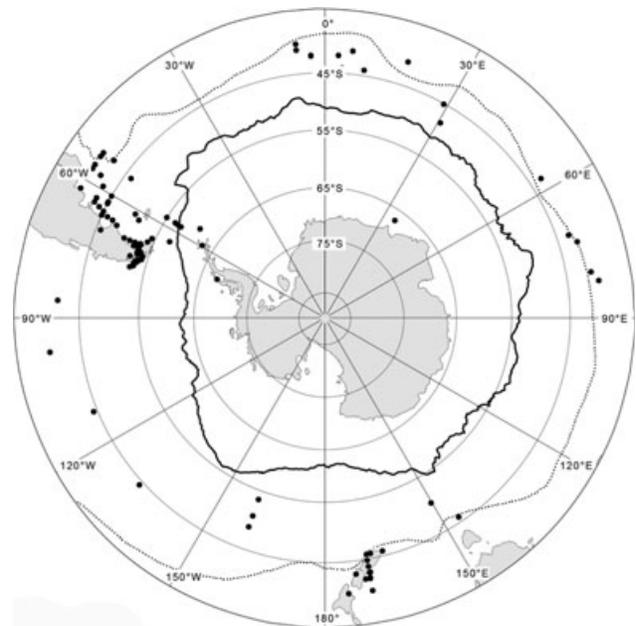


Fig. 8. The locations from which no Southern Ocean endemic species, only widespread species were reported. Out of the 402 Southern Ocean sites sampled, from 115 sites only widespread species were reported. These Southern Ocean sites, from which no endemic species were reported, are located largely in the northern portion of the Southern Ocean.

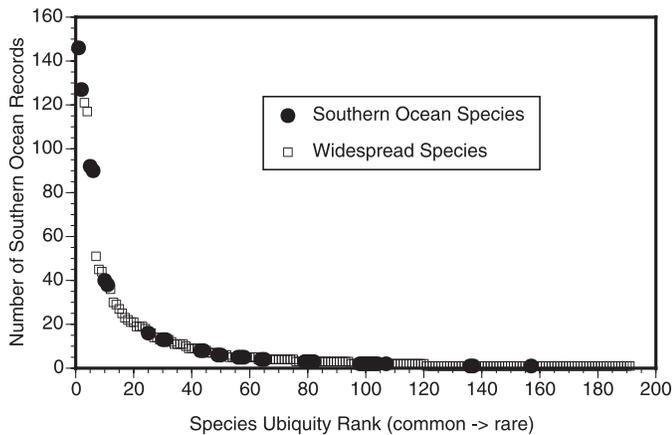


Fig. 6. Species ubiquity rank graph. The number of sites from each species has been recorded defines its ubiquity. The species are then ordered by ubiquity, from most common to rare, and each plotted against the number of records for the species. Note that both Southern Ocean endemic species and widespread species are among the most and least common forms reported.

Ocean appears to be distributed bimodally with peaks at about 45 and 120 μm and an absence of species with oral diameters of 70–90 μm . The most common size classes of oral diameters are between 40 and 50 μm suggesting that most species likely exploit prey of 10–15 μm in size with the second peak of large-mouthed forms exploiting prey of about

30 μm in size. Among the tintinnids of the Southern Ocean, the endemic species appear to show a characteristic, which distinguishes them from the widespread species found in the Southern Ocean. A large portion of the endemic species have

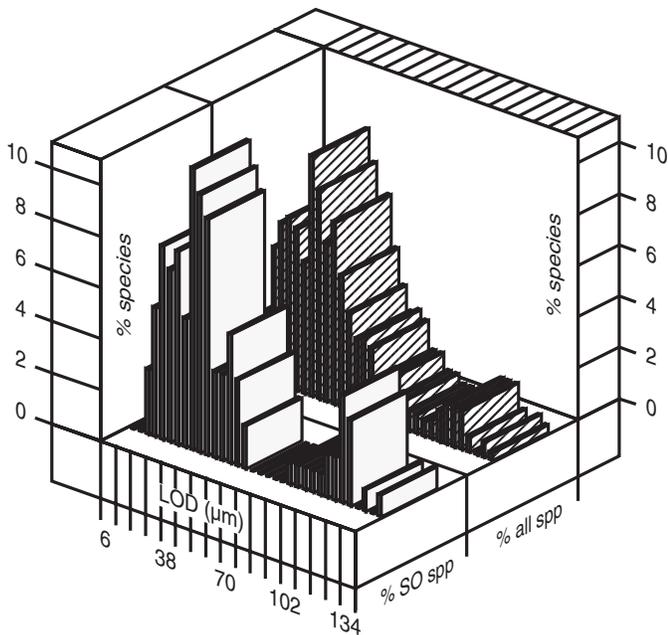


Fig. 9. Distributions of the lorica oral diameters of the species found in the Southern Ocean (120 species excluding strays) appears largely similar to that of the overall species catalog of tintinnid species, of about 700 described in Kofoid and Campbell (1929, 1939).

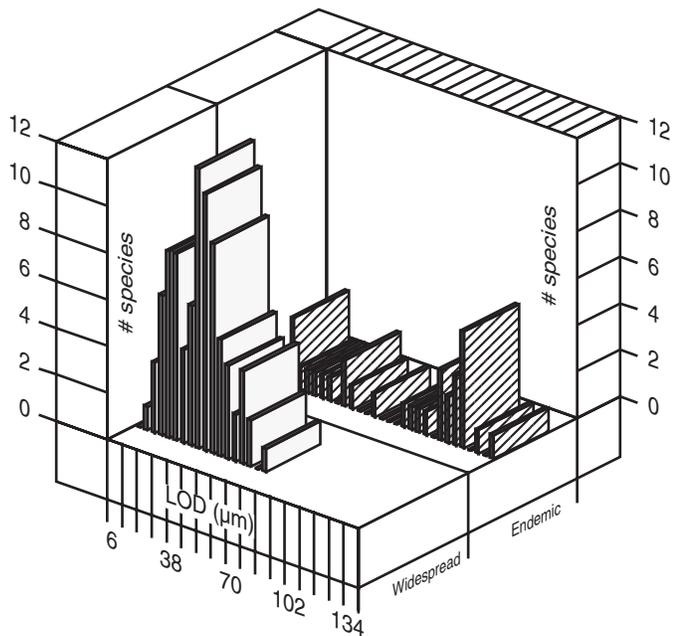


Fig. 10. Distributions of the lorica oral diameters of the widespread species found in the Southern Ocean and the Southern Ocean endemic species. The assemblage of endemic species appears distinct from that of the widespread species in terms of typical oral diameters, presumably reflecting exploitation of different sizes of prey items.

large oral diameters ($> 100 \mu\text{m}$), whereas most of the widespread species have oral diameters between 40 and 60 μm in size (Fig. 10).

The species typical of the Southern Ocean includes some, which agglutinate particulate matter into the lorica, for exam-

ple species of *Laackmaniella* and *Stenosomella*. Agglutination may appear to be highly selective as has long been known for some species of *Codonella* and *Dictyocysta*, which symmetrically arranged coccoliths from a few species of coccolithophoride phytoplankton (e.g. Lohmann 1912). However, *Laackmaniella* uses frustules from several different diatom species (Fig. 1). At least with regard to *Stenosomella*, the type of particle used, coccoliths or diatom remains, seems to simply reflect their relative abundance in the water column (Henjes and Assmy 2008).

COMPARISON WITH ARCTIC TINTINNIDS

Kofoid was perhaps the first to remark that in the "circumpolar seas" tintinnid abundances can be high, but species richness appears quite low and that this is the exact opposite of tropical seas where abundance is low, but species richness is high; interestingly, he attributed the difference to a temperature effect on mutation rate and consequently higher rates of speciation in warmer waters (Kofoid 1930). Beyond harboring relatively few species, there are some striking similarities comparing the Arctic and Southern Oceans. Like the Southern Ocean assemblages, the tintinnid fauna of the Arctic Biome is a mixture of forms apparently restricted to the biome, species of the genera *Parafavella* and *Ptychocyclus* as well as many widespread species (e.g. Burkovsky 1976). Many of the widespread species found in Arctic assemblages are also common in the Southern Ocean, such as *Helicostomella subulata* and *Codonellopsis pusilla*. Both Arctic and Antarctic assemblages contain the "bipolar" species *Acanthostomella norvegica*.

One of the peculiarities of tintinnid genera apparently restricted to the Arctic, species of the genera *Parafavella* and *Ptychocyclus*, is shared by the Antarctic genera *Cymatocyclus* and *Laackmanniella*. The genera all contain large numbers of different morphotypes, distinguished as species for the most part. These different morphologies can be shown to be a continuum, at least with regard to forms of *Cymatocyclus* (Williams et al. 1994). Recent genetic data has shown that the different morphotypes have identical ssRNA sequences in both *Cymatocyclus* species as well as in varieties of *Laackmanniella* (Kim S. Y., Choi J. K., Dolan J. R., Shin H. C., Lee S.-H. & Yang E. J., unpubl. data). Thus, at least with regard to the Southern Ocean, the endemic forms appear to be highly polymorphic with only the lorica oral diameter as a consistent, conservative, character. It is likely that the Arctic forms, species of *Parafavella* and *Ptychocyclus* will also prove to be polymorphic; to date, no genetic studies have been conducted. Unfortunately, the mechanisms underlying polymorphism remain unknown. In both Arctic and Antarctic assemblages, "coxiella" forms are often abundant (e.g. Brandini 1993; Burkovsky 1976). The coxiella form often appears to be an aberrant morphology of a not fully developed lorica, perhaps characteristic of a rapidly growing population (Laval-Peuto 1977). Speculatively, we suggest that polymorphism in the Antarctic taxa 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.

CONCLUSIONS AND SUGGESTIONS FOR FUTURE WORK

Tintinnids are at once a typical and unusual group of organisms for the Southern Ocean. As is the case for many taxa, there are genera and species of tintinnids found only in the Southern Ocean as well as bipolar species and many species found in the Southern Ocean are commonly considered

cosmopolitan or widespread. The assemblage remains unusual in terms of species richness, especially considering that tintinnids represent a very small portion, usually less than 10% of individuals, of the functional group of microzooplankton. The assemblage also remains unusual as very large forms, species of *Cymatocylis*, are common and polymorphic species seem to be relatively common as well. Endemic species, those restricted to the Southern Ocean can be distinguished from widespread species of tintinnids found in the Southern Ocean. In terms of geographic distribution, endemics are often the only forms found in sites near Antarctica and many are characterized by unusually large oral diameters (Fig. 7). While we can make general statements concerning distributions and morphology, unfortunately, we lack the most basic data on the ecology of individual species and the assemblage as a whole. For example, there are no data whatsoever concerning growth rates nor feeding rates of species from the Southern Ocean. Such a lack of data considerably complicates the examination of fundamental questions, which well merit examination. How can so many different forms successfully exploit waters of extreme seasonality? Is polymorphism an adaptation to or rather a consequence of a variable environment? Will changes in the extent of winter ice coverage influence the distributions of tintinnids? We can only hope that future field study in Southern Ocean waters will include special attention to these intriguing organisms, which are often neglected (e.g. Griffiths 2010).

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LITERATURE CITED

- Agatha, S. 2011. Global diversity of aloricate Oligotrichea (Protista, Ciliophora, Spirotricha) in marine and brackish sea water. *PLoS ONE*, **6**:e22466, doi: 10.1371/journal.pone.
- Agatha, S. & Strüder-Kypke, M. C. 2012. Reconciling cladistics and genetic analyses in choreotrichid ciliates (Ciliophora, Spirotricha, Oligotrichea). *J. Eukaryot. Microbiol.*, **59**:325–350.
- Agatha, S., Strüder-Kypke, M. C. & Beran, A. 2004. Morphologic and genetic variability in the marine planktonic ciliate *Laboea strobila* Lohmann 1908 (Ciliophora, Oligotrichia), with notes on its ontogenesis. *J. Eukaryot. Microbiol.*, **51**:267–281.
- Armand, L. K., Crosta, X., Romero, O. & Pichon, J.-J. 2005. The biogeography of major diatom taxa in Southern Ocean sediments: 1. Sea ice related species. *Paleoeco. Paleoclimat. Paleoecol.*, **223**:93–126.
- Bachy, C., Gomez, F., Lopez-Garcia, P., Dolan, J. R. & Moreira, D. 2012. Molecular phylogeny of tintinnid ciliates (Tintinnida, Ciliophora). *Protist*, **163**:873–887.
- Brandini, F. P. 1993. Phytoplankton biomass on an Antarctic coastal environment during stable water conditions – implications for the iron limitation theory. *Mar. Ecol. Prog. Ser.*, **93**:267–275.
- Brökeland, W., Guomundsson, G. & Svavarsson, J. 2010. Diet of four species of deep-sea isopods (Crustacea: Malacostraca: Peracarida) in the South Atlantic and the Southern Ocean. *Mar. Biol.*, **157**:177–187.
- 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. *Antarct. Sci.*, **4**:3–98.
- Burkill, P. H., Edwards, E. S. & Sleight, M. A. 1995. Microzooplankton and their role in controlling phytoplankton growth in the marginal ice zone of the Bellingshausen Sea. *Deep-Sea Res. II*, **42**:1277–1290.
- Burkovsky, I. V. 1976. New data on tintinnids (Ciliata) of the Arctic and revision of fauna. *Zoologicheskii Zhurnal*, **55**:325–336.
- Calbet, A. & Landry, M. R. 2004. Phytoplankton growth, microzooplankton grazing, and carbon cycling in marine systems. *Limnol. Oceanogr.*, **49**:51–57.
- Caron, D. A., Denett, M. R., Lonsdale, D. J., Moran, D. M. & Shalapyonok, L. 2000. Microzooplankton herbivory in the Ross Sea, Antarctica. *Deep-Sea Res. II*, **47**:3249–3272.
- Cleve, P. T. 1900. Plankton from the southern Atlantic and the southern Indian Ocean. *Ofversigt af Kongl. Vetenskaps-Akademiens Förhandlingar*, **57**:919–938.
- Crosta, X., Romero, O., Armand, L. K. & Pichon, J.-J. 2005. The biogeography of major diatom taxa in Southern Ocean sediments: 2. Open ocean related species. *Paleoeco. Paleoclimat. Paleoecol.*, **223**:66–92.
- Darling, K. F., Kucera, M. & Wade, C. M. 2007. Global molecular phylogeography reveals persistent Arctic circumpolar isolation in a marine planktonic protist. *Proc. Nat. Acad. Sci. U.S.A.*, **104**:5002–5007.
- Deacon, G. 1984. The Antarctic Circumpolar Ocean. Cambridge University Press, Cambridge, U.K.
- Dolan, J. R. 2010. Morphology and ecology in tintinnid ciliates of the marine plankton: correlates of lorica dimensions. *Acta Protozool.*, **49**:235–344.
- Dolan, J. R. & Stoeck, T. 2011. Repeated sampling reveals differential variability in measures of species richness and community composition in planktonic protists. *Environ. Microbiol. Rep.*, **3**:661–666.
- Dolan, J. R., Ritchie, M. E., Tunin-Ley, A. & Pizay, M. 2009. Dynamics of core and occasional species in the marine plankton: tintinnid ciliates in the northwest Mediterranean Sea. *J. Biogeogr.*, **36**:887–895.
- Fonda Umani, S., Monti, M., Cataletto, B. & Budillon, G. 2011. Tintinnid distributions in the Strait of Magellan (Chile). *Polar Biol.*, **34**:1285–1299.
- Fontaneto, D. & Brodie, J. 2011. Why biogeography of microorganisms? In: Fontaneto, D. (ed.), *Biogeography of Microorganisms: Is Everything Small Everywhere?* Cambridge University Press, Cambridge, U.K. p. 3–10.
- Froneman, P. W. 2004. Protozooplankton community structure and grazing impact in the eastern Atlantic sector of the Southern Ocean in austral summer 1998. *Deep-Sea Res. II*, **51**:2633–2643.
- Gaston, K. J. & Spicer, J. I. 2003. *Biodiversity: An Introduction*, 2nd ed. Blackwell Publishing, Oxford, U.K.
- Griffiths, H. J. 2010. Antarctic marine biodiversity – what do we know about the distribution of life in the Southern Ocean? *PLoS ONE*, **5**:e11683, doi: 10.1371/journal.pone.0011683.
- Hall, M. S. & Katz, L. A. 2011. On the nature of species: insights from *Paramecium* and other ciliates. *Genetica*, **139**:677–684.
- Heinbokel, J. F. 1978. Studies on the functional role of tintinnids in the southern California Bight. I. Grazing and growth rates in laboratory cultures. *Mar. Biol.*, **47**:177–189.
- Henjes, J. & Assmy, P. 2008. Particle availability controls agglutination in pelagic tintinnids in the Southern Ocean. *Protist*, **159**:239–250.
- Hopkins, T. L. 1987. Midwater food web in McMurdo Sound, Ross Sea, Antarctica. *Mar. Biol.*, **96**:93–106.
- Karayanni, H., Christaki, U., Van Wambeke, F., Denis, M. & Moutin, T. 2005. Influence of ciliated protozoa and heterotrophic nanoflagellates on the fate of primary production in the northeast Atlantic Ocean. *J. Geophys. Res.*, **110**:C07S15.
- Katz, L. A., McManus, G. B., Snoeyenbos-West, O. L. O., Griffin, A., Pirog, K., Costas, B. & Foissner, W. 2005. Reframing the ‘Everything is everywhere’ debate: evidence for high gene flow and diversity in ciliate morphospecies. *Aquat. Microb. Ecol.*, **4**:55–65.
- Kellermann, A. 1987. Food and feeding ecology of postlarval and juvenile *Pleurogramma antarcticum* (Pisces; Notothenioidei) in the seasonal pack ice zone off the Antarctic Peninsula. *Polar Biol.*, **7**:307–315.
- Kim, S. Y., Yang, E. J., Gong, J. & Choi, J. K. 2010. Redescription of *Favella ehrenbergii* (Claparède and Lachmann, 1858) Jörgensen, 1924 (Ciliophora: Choreotrichia), with phylogenetic analyses based on small subunit rRNA gene sequences. *J. Eukaryot. Microbiol.*, **57**:460–467.
- Kofoed, C. A. 1930. Factors in the evolution of the Tintinninoidea. In: *Contributions to Marine Biology, Lectures and Symposia Given at the Hopkins Marine Station, December 20–21, 1929, at the Mid-*

- winter Meeting of the Western Society of Naturalists. Stanford University Press, Stanford, CA, USA. p. 1–39.
- Kofoed, C. A. & Campbell, A. S. 1929. A conspectus of the marine and freshwater Ciliata belonging to the suborder Tintinnoinea, with descriptions of new species principally from the Agassiz expedition to the Eastern Tropical Pacific 1904–1905. *Univ. Calif. Publ. Zool.*, **34**:1–403.
- Kofoed, C. A. & Campbell, A. S. 1939. Reports on the scientific results of the expedition to the Eastern Tropical Pacific, in charge to Alexander Agassiz, by U.S. Fish Commission Steamer “Albatross” from October 1904 to March 1905, Lieut. Commander L.M. Garrett, U.S.N. commanding. 37. The Ciliata: The Tintinnoinea. *Bull. Mus. Comp. Zool., Harv. Univ.*, **84**:1–473.
- Kruse, S., Jansen, S., Krägersky, S. & Bathman, U. 2009. Gut content analysis of three dominant Antarctic copepod species during an induced phytoplankton bloom EIFEX (European iron fertilization experiment). *Mar. Ecol.*, **30**:301–312.
- Laackmann, H. 1907. Antarktische Tintinnen. *Zool. Anzeig.*, **31**:235–239.
- Laackmann, H. 1910. Die Tintinnodean der Deutschen Südpolar-expedition 1901–1903. *Deutsche Südpolar-Expedition. XI. Zoologie III*, **11**:340–396.
- Laval-Peuto, M. 1977. Reconstruction d’une lorica de forme *Coxiella* par le trophonte nu de *Favella ehrenbergii* (Ciliata, Tintinnina). *Compt. Rend. Hebdom. Seanc. Acad. Sci. Paris, Sér. D.*, **284**:547–550.
- Laval-Peuto, M. & Brownlee, D. C. 1986. Identification and systematics of the Tintinnina (Ciliophora): evaluation and suggestion for improvement. *Ann. Inst. Océanogr., Paris*, **62**:69–84.
- Li, Z., Yi, Z., Yang, J., Gong, J., Clamp, J. C., Rasheid, K. A. S., Al-Arifi, S., Al-Khedhairi, A. A. & Song, W. 2009. Phylogenetic investigation on five genera of tintinnid ciliates (Ciliophora, Choreotrichia), based on the small subunit ribosomal RNA gene sequences. *Prog. Nat. Sci.*, **19**:1097–1101.
- Lohmann, H. 1912. Beiträge zur charakterisierung des tier- und pflanzlebens in den von ‘Deutschland’ während ihrer fahrt nach Buenos Ayres durchfahrenen gebieten des Atlantischen Ozeans. II. Teil. *Int. Rev. Ges. Hydrobiol. Hydrogr.*, **5**:185–225.
- Longhurst, A. 1998. Ecological Geography of the Sea. Academic Press, San Diego, CA, USA.
- Lonsdale, D. J., Caron, D. A., Dennett, M. R. & Schaffner, R. 2000. Predation by *Oithona* spp. on protozooplankton in the Ross Sea, Antarctica. *Deep-Sea Res. II*, **47**:3273–3283.
- Mauchline, J. 1980. The biology of mysids and euphausiids. *Adv. Mar. Biol.*, **18**:3–681.
- Orejas, C., Gili, J.-M. & Arntz, W. 2003. Role of small-plankton communities in the diet of two Antarctic octocorals (*Primnoisis antarctica* and *Primnoella* sp.). *Mar. Ecol. Prog. Ser.*, **250**:105–116.
- Pierce, R. W. & Turner, J. T. 1993. Global biogeography of marine tintinnids. *Mar. Ecol. Prog. Ser.*, **94**:11–26.
- Romero, O. E., Armand, L. K., Crosta, X. & Pichon, J. J. 2005. The biogeography of major diatom taxa in Southern Ocean surface sediments: 3. Tropical/Subtropical species. *Paleoecol. PaleoClimat.*, **223**:49–65.
- Saccà, A., Strüder-Kype, M. C. & Lynn, D. H. 2012. Redescription of *Rhizodanus tagatzi* (Ciliophora: Spirotrichea: Tintinnida), based on morphology and small subunit ribosomal RNA gene sequence. *J. Eukaryot. Microbiol.*, **59**:218–231.
- Santoferrara, L. F., McManus, G. B. & Alder, V. A. 2012a. Utility of genetic markers and morphology for species discrimination within the order Tintinnida (Ciliophora, Spirotrichea). *Protist*, **163**: (in press)
- Santoferrara, L. F., McManus, G. B. & Alder, V. A. 2012b. Phylogeny of the order Tintinnida (Ciliophora, Spirotrichea) inferred from small- and large-subunit rRNA genes. *J. Eukaryot. Microbiol.*, **59**:423–426.
- Tsuda, A. & Kawaguchi, S. 1997. Microzooplankton grazing in the surface water of the Southern Ocean during an austral summer. *Polar Biol.*, **18**:240–245.
- Wickham, S. A., Steinmair, U. & Kamennaya, N. 2011. Ciliate distributions and forcing factors in the Amundsen and Bellingshausen Seas (Antarctica). *Aquat. Microb. Ecol.*, **62**:215–230.
- Williams, R., McCall, H., Pierce, R. W. & Turner, J. T. 1994. Speciation of the tintinnid genus *Cymatocylis* by morphometric analysis of the loricae. *Mar. Ecol. Prog. Ser.*, **107**:263–272.
- Xu, D., Sun, P., Shin, M. K. & Kim, Y. O. 2012. Species boundaries in tintinnid ciliates: a case study – morphometric variability, molecular characterization, and temporal distribution of *Helicostomella* species (Ciliophora, Tintinnina). *J. Eukaryot. Microbiol.*, **59**:351–358.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Sources of tintinnid species records for the Southern Ocean.

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