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Abundance and distribution of tintinnid ciliates in an ice edge zone during the austral autumn

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Abstract: Tintinnid ciliates were present throughout the upper (100m) water column of the ice-edge zone when sampled in autumn 1986 in the Weddell Sea. Biomass ranged from 0.02 μgC l^{-1} under the sea-ice to 1.3 μgC l^{-1} in the ice-free water column. *Cymatocylis*, *Codonellopsis*, *Laackmaniella* and a small *Salpingella* were the most abundant and/or largest biomass contributors. The under ice assemblage was characterized by low biomass and dominated by small species (*Salpingella* and *Codonellopsis*); the ice edge stations were dominated by these same taxa but in higher abundances while the open water assemblage was characterized by high biomass and dominated by *Cymatocylis*, the largest taxa. All taxa exhibited maximum concentrations in the upper 50m of the water column. Both krill and salps grazed upon the *Cymatocylis* and *Codonellopsis* without preference in both the ice covered and open water regimes.

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Introduction

Tintinnid ciliates have been studied in Antarctic waters from the earliest scientific expeditions (Laackmann 1910). Much of the work has focused on the taxonomy and morphology of their distinctive loricas (Kofoid & Campbell 1929, Hada 1961, 1969, Balech 1973, van der Spoel 1986, Boltovskoy *et al.* 1990). Quantitative information is available from a variety of Antarctic environs including coastal embayments (Littlepage 1969, Heinbokel & Coats 1985), neritic waters (Hopkins 1985, Adler & Boltovskoy 1991), the open water off the sea ice edge (Hentschel 1936, Hewes *et al.* 1985, Heinbokel & Coats 1986, Boltovskoy *et al.* 1989) and in sea ice covered regions (Gowing & Garrison 1991, Boltovskoy *et al.* 1989).

Current interest in tintinnid ciliates stems from their potential role in marine food webs. Tintinnids may be an intermediate link in food webs because they have the capacity to graze pico- and nano- sized phytoplankton which are not efficiently grazed by larger consumers such as *Euphausia superba* Dana (Quetin & Ross 1985). The Antarctic sea-ice edge zone is well suited to examining these relationships because of gradients in primary and secondary production across this boundary (Nelson *et al.* 1987, 1989, Garrison & Buck 1989).

The objective of our study was to determine the abundance, biomass and composition of the tintinnid assemblage in the upper water column of the ice edge zone during the austral autumn. The distributional patterns that emerged are examined in relation to earlier works and to potential food sources and predators.

Materials and methods

The AMERIEZ (Antarctic Marine Ecosystem Research in the Ice Edge Zone) study site and stations analyzed for this study are located between latitudes 65–66°S and longitudes 42–50°W (Garrison & Buck 1989). Stations seaward of the ice edge (M17–M24) were sampled by the RV *Melville* 13–16 March 1986 and those under the sea-ice (G14–G12) were sampled from the USCGC *Glacier* 13–15 March 1986 (Sullivan & Ainley 1987). Stations M19–24 are treated as open water stations, M17 and G12 as ice edge stations and G13 and G14 as under ice stations. At each station 30 l of seawater was collected from each of five or six depths in the upper 100 m of the water column with Niskin sampling bottles. Samples used for abundance estimates of the larger and rarer forms were processed in two different manners. One technique involved pouring the contents of the sample bottle through a 30 μm mesh sieve and washing the contents into a bottle. These samples were preserved with formalin (5% final concentration) and loricae were counted under a dissection microscope at a magnification of 50X. The second technique involved concentrating 12–20 l by reverse-flow filtration through 20 μm mesh (Dodson & Thomas 1978) to 200–500 ml. These samples were preserved in Karnovsky's solution(Gold 1976) and an aliquot of 10 to 100 ml counted on an inverted compound microscope using the Utermöhl technique (Reid 1983) at a magnification of 150X. Full and empty loricas were differentiated from one another in these samples and measurements made on the protoplasts were converted to biovolume and subsequently to carbon using the conversion of Putt & Stoecker (1989)

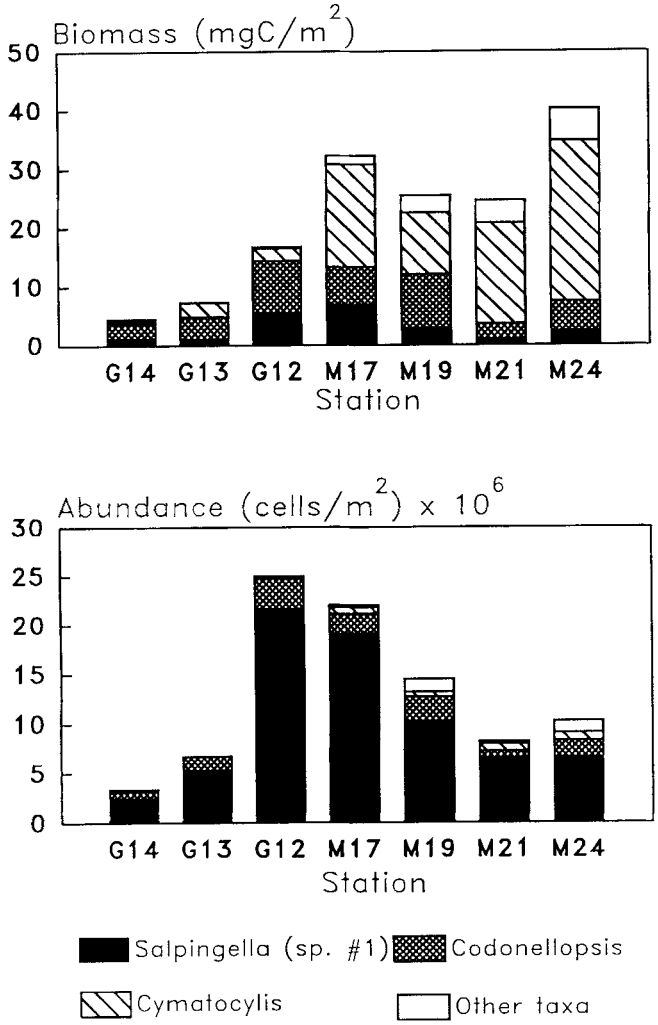

Fig. 1. Integrated biomass (mgC m^{-2}) and abundance (cells m^{-2}) of *Salpingella* (sp. #1), *Codonellopsis*, *Cymatocylis* and other taxa at seven stations sampled across the ice-edge zone in March 1986.

(pgC=volume (μm^3) x 0.14). Only the biomass of protoplasts were used, the carbon value of the loricae was not calculated or included in the biomass results. On average the equivalent of 3.5 l (range 0.4–8.0 l) of the reverse flow samples was counted to obtain the estimates used in this study. Abundance and biomass estimates for the smaller and more numerous *Salpingella* (sp.#1) were made from unconcentrated 40 or 80 ml samples preserved with Karnovsky's solution and counted on an inverted microscope. An average of 54 (2–269) full loricae (sum of reverse flow concentrated and unconcentrated counts) were enumerated for each depth analyzed. *Codonellopsis* and *Cymatocylis* were considered monospecific genera following the conventions of Laackmann(1910), Balech (1973) and van der Spoel (1986).

Gut contents of *Salpa thompsonii* and *Euphausia superba* from open water and under the pack ice were analysed for tintinnid loricae (Hopkins 1985). *Euphausia* was obtained from the ship's intake in open water or from the stomachs of seals in pack ice to circumvent the effects of feeding in the net. Salps were collected with plankton nets.

Table I. Abundance, biomass and biovolume estimates for six taxa of tintinnid ciliates and total tintinnid ciliates from the ice edge zone of the Weddell Sea during Mar. 1986. Standard deviations given for the total tintinnid assemblage. *n* is the number of samples in which the taxon was observed.

	n	Abundance (cells l^{-1}) max	mean	Biomass (μgC l^{-1}) max	mean	Mean biovolume (μm^3)
Salpingella (sp. #1)	33	380	110	0.32	0.07	4600
Laackmaniella	21	24	2.1	0.19	0.04	13000
Salpingella (sp. #2)	19	27	3.6	0.05	0.01	14000
Codonellopsis	34	96	12.0	0.46	0.09	40000
Coxliella	17	25	4.6	0.18	0.03	46000
Cymatocylis	26	72	5.4	0.89	0.18	380000
Total	35	445	130±120	1.31	0.39±0.39	

Results

Tintinnid ciliates were found throughout the upper 100 m of the water column in the study area. Biomass and abundance estimates ranged from <.02 μgC l^{-1} and <1 cell l^{-1} at 100 m under ice to 1.31 μg C l^{-1} ($\bar{x}$ = 0.39 ± 0.39) and 445 cells l^{-1} ($\bar{x}$ = 130 ± 120) at the surface in open water (Table I). Integrated abundance in the upper 100 m ranged from 3.3x10^6 cells m^{-2} at G14 to 2.5x10^7 cells m^{-2} at the ice edge station G12 (Fig. 1). Integrated biomass ranged from 7.7 mgC m^{-2} at G14 to 70.2 mgC m^{-2} at M24 (Fig. 1). Biomass was higher in the upper 50 m of open water than in the interval from 50–100m, but no such difference occurred at ice edge or under ice stations(Table II).

Biovolume of the taxa recorded ranged from 4.6x10^3 to 3.8x10^5 μm^3 (Table I). The smallest species, an unidentified *Salpingella* (sp. #1)(approximately 65 μm x 10 μm, Fig. 2), was the most abundant tintinnid ciliate (Table I) accounting for the abundance maximum at station G12 (Fig. 1). Its size and general appearance matches that of the unnamed species referred to in Heinbokel & Coates (1985). The largest taxa, *Cymatocylis*, comprised most of the tintinnid biomass at the open water stations. *Codonellopsis*, while not as important in biomass or abundance, was present in most samples and contributed most of the biomass at G14 and G13. *Laackmaniella*, another larger unidentified *Salpingella* (sp. #2) and an unidentified species of *Coxliella* occurred sporadically (Tables I & II, Fig. 1).

Several of the taxa exhibited specific patterns of distribution. *Cymatocylis* was more abundant in the upper 50 m than from

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Table II. Vertical and horizontal distribution of four species and of total tintinnid ciliates. Values are means with standard deviations (cells m^{-2} or mgC m^{-2}) of the integrated upper and lower 50 m of the water column for ice covered G14 and G13 (Ice), ice edge G12 and M17 (Edge) and open water stations, M19–M24 (Water).

	Depth interval					
	0–50m			50–100m		
	Ice	Edge	Water	Ice	Edge	Water
Salpingella (sp. #1)	$3.0x10^6$ ± $2.7x10^6$	$1.7x10^7$ ± $5.1x10^6$	$5.3x10^6$ ± $2.5x10^6$	$9.0x10^5$ ± $6.4x10^5$	$3.5x10^6$ ± $3.2x10^6$	$2.3x10^6$ ± $9.6x10^5$
Laackmaniella	$3.2x10^3$ ± $4.5x10^3$	$3.8x10^4$ ± $5.4x10^4$	$1.8x10^5$ ± $1.4x10^5$	$5.6x10^4$ ± $6.3x10^4$	$4.4x10^4$ ± $6.0x10^4$	$3.8x10^4$ ± $3.0x10^4$
Codonellopsis	$5.4x10^5$ ± $1.6x10^4$	$1.1x10^6$ ± $7.6x10^5$	$1.3x10^6$ ± $8.4x10^5$	$4.4x10^5$ ± $4.1x10^5$	$1.3x10^6$ ± $1.4x10^6$	$2.5x10^5$ ± $2.7x10^4$
Cymatocylis	$2.6x10^4$ ± $1.6x10^4$	$1.9x10^5$ ± $1.8x10^5$	$5.0x10^5$ ± $1.8x10^5$	$1.7x10^4$ ± $2.3x10^4$	$1.5x10^5$ ± $1.5x10^5$	$1.4x10^5$ ± $2.6x10^4$
Total	$3.7x10^6$ ± $2.7x10^6$	$1.8x10^7$ ± $4.1x10^6$	$7.9x10^6$ ± $3.6x10^6$	$1.4x10^6$ ± $2.5x10^6$	$5.0x10^6$ ± $2.0x10^6$	$3.2x10^6$ ± $2.8x10^6$
Total Biomass	3.4 ± 0.7	15.1 ± 11.2	23.6 ± 5.7	2.4 ± 1.4	9.5 ± 0.1	6.5 ± 2.9

50 to 100 m in the open water (Table II). Under ice cover and at the ice edge, however, no differences in abundance between the two depth intervals occurred. The integrated abundances (0–100 m) of *Cymatocylis* in open water were higher than at comparable intervals under the ice (Table II). The highest abundances of *Salpingella* sp. #1 occurred in the upper 50 m of the ice edge stations; abundances elsewhere were significantly lower. The abundance of *Codonellopsis* in the upper 50 m of open water and ice edge stations was also higher than that under sea-ice (Table II); lowest abundances of this group were found in the 50–100m depth interval of open water.

Diet analyses of *Salpa thompsonii* and *Euphausia superba* indicate that these two metazoans consistently ingest tintinnid ciliates in the open water and under the ice (Table III). The ratio of *Cymatocylis* to *Codonellopsis* loricae in the guts of both metazoans in the open water and under ice reflected the *in situ* ratio of their loricae in the two habitats (Table III). A comparison of direct sieving through 30 μm mesh and reverse flow concentration with 20 μm mesh net revealed no significant differences (paired sample *t*-test, $P>0.05$) in abundance estimates for *Cymatocylis* (Table IV). Abundance estimates of *Codonellopsis* from reverse flow concentration using 20 μm mesh however, were significantly higher (paired sample *t*-test, $P>0.05$) than those obtained from direct sieving (reverse flow =303% sieving).

Discussion

Tintinnid ciliates were present throughout our study area at biomasses that ranged over several orders of magnitude. A comparison of our data with other tintinnid studies carried out in Antarctic waters indicates general agreement of biomass estimates (Table V), particularly when a comparable conversion (Putt & Stoecker 1989) is used. Our biomass estimates of open water in comparable latitudinal regions are lower than those reported by Boltovskoy *et al.* (1989). Corresponding abundances of full as well as total (full + empty) loricae of the three taxa in common, however, are similar (Table V). Since tintinnid ciliates are capable of abandoning their loricae (V. A. Alder & D. Boltovskoy, personal communication 1990), biomass estimates based on full loricae may be underestimates. Naked oligotrichous ciliates of a size and morphology similar to that found in loricae of *Cymatocylis* were present in most samples and

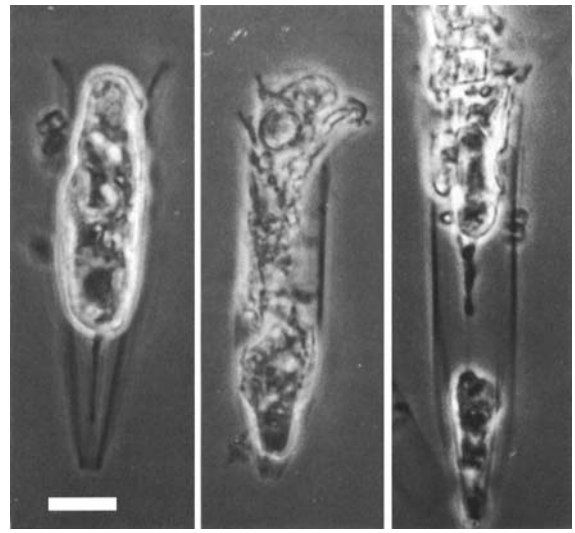

Fig. 2. Three loricae with protoplasts of the small *Salpingella* (sp. #1) collected from ice edge stations. Scale bar = 10μm.

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Table III. *Cymatocylis* and *Codonellopsis* as mean (± standard deviation) relative percent abundance in the stomachs of *Salpa thompsonii* and *Euphausia superba* and in the water column of USCGC *Glacier* sampled stations (G12–G14) and RV *Melville* sampled stations (M17–M24). *n* = number of stomachs analysed.

	Open water			Ice covered		
	Cymatocylis	*n*	*Codonellopsis*	*Cymatocylis*	*n*	*Codonellopsis*
Salpa	38.3±16.5	25	57.2±16.9	6.5±7.8	22	84.1±15.8
Euphausia	47.5±35.5	31	52.2±35.1	12.4±14.3	32	67.6±29.0
Water column	28.6±15.1		63.9±16.9	3.4±1.6		90.9±16.9

Table IV. Comparison of abundance estimates (loricae m^{-3}) from 30 μm direct sieving and 20 μm reverse flow concentration techniques for *Cymatocylis* and *Codonellopsis*.

Station	*Cymatocylis*		*Codonellopsis*	
	Sieving	Reverse flow	Sieving	Reverse flow
M17	$1.4x10^6$	$1.1x10^6$	$2.1x10^6$	$4.4x10^6$
M19	$1.7x10^6$	$1.1x10^6$	$1.6x10^6$	$5.7x10^6$
M21	$7.3x10^5$	$9.6x10^5$	$7.5x10^5$	$1.8x10^6$
M24	$1.5x10^6$	$1.3x10^6$	$6.8x10^5$	$3.6x10^6$

could account for up to 20% of the total tintinnid biomass (unpublished data). Use of a volume to carbon regression equation that takes into account the lorica carbon (Verity & Langdon 1984, Gilron & Lynn 1989) would also increase our biomass estimates.

A comparison of our abundance data with other studies suggests that most studies have missed the most abundant tintinnid in Antarctic waters, the small species *Salpingella* sp. #1 (Fig. 2) that occurred in our study and in the study by Heinbokel & Coats (1985). We have shown that the use of 30–35 μm mesh to concentrate tintinnid ciliates (Hopkins 1985, Heinbokel & Coats 1986) seriously underestimates the abundances of *Codonellopsis* (Table IV). Although *Salpingella* sp. #1 was present in the 20 μm mesh reverse flow concentrated samples (unpublished data), the abundance estimates based through this technique are much lower than in settled whole water samples. Epifluorescence microscopy (Hewes *et al.* 1985) of whole water samples filtered upon membrane filters could also be used to estimate the abundance of this taxa. A two tiered counting strategy, using both unconcentrated and concentrated samples may be necessary to accurately assess the abundance of a tintinnid ciliate assemblage that spans such a large size and abundance range (Table I).

Our study shows that three tintinnid populations occur in the region of the ice edge zone. The under ice population is characterized by low abundances and biomass, is distributed evenly throughout the water column (Fig. 3, Table II) and is dominated by *Codonellopsis* and the small *Salpingella* sp. #1. Biomass at the under ice stations, G14 and G13, is lower than reported previously for the austral summer, but it is several orders of magnitude higher than that reported for the austral winter under ice stations (Gowing & Garrison 1991, Table V). The ice edge stations of G12 and M17 were characterized by the highest abundances found during this study and higher biomass than at the ice covered stations (Fig. 1). *Salpingella* sp. #1 is the numerical dominant (Fig. 1). The open water stations, M19–M24, had lower abundances than ice edge stations but were higher in biomass. The biomass at the open water stations was concentrated in the upper 50 m and was dominated by *Cymatocylis* (Fig. 1, Table II). The lack of both movement of the ice edge and advection in our study site during our presence there (Sullivan *et al.* 1988), combined with a low phytoplankton biomass and high biogenic silica to particulate organic carbon ratios led Nelson *et al.* (1989) to hypothesize that the system was in its post phytoplankton bloom phase and dominated by heterotrophic processes. Microzooplankton assemblages should therefore be well developed, and the assemblages we report from the open water (high biomass of large taxa) may be representative of well developed open water tintinnid populations.

The changes in tintinnid assemblages and biomass must be related to food resources (Smith 1987) and their predators. The positive and significant correlations between tintinnid biomass and phytoplankton (Garrison & Buck 1989) indicates tintinnids may be responding to relatively small abundance shifts (0.1–0.4 mg chl *a* m^{-3}) in their prey. Adler & Boltovskoy (1991) substantiate this by reporting positive correlations between tintinnids and potential food sources (microplanktonic settling volumes) as well as with competing grazers (thecate dinoflagellates, mostly *Protoperidinium*). Tintinnids, in the abundances reported here, (which seem to be typical of austral summer concentrations), and at reported grazing rates (Garrison & Buck 1989), can only graze a minor fraction of the daily production. Other components of the heterotrophic assemblage, possibly small athecate and larger thecate dinoflagellates (Garrison *et al.* 1991, Boltovskoy *et al.* 1989) may make a more significant impact upon the phytoplankton production. The occurrence of loricae of both *Codonellopsis* and *Cymatocylis* in the guts of both *Euphausia* and *Salpa* in the same proportion as their abundance in the water column (Table III) indicates that grazing may affect biomass levels achieved, but probably not the assemblage composition measured the larger loricae. Loricae of the small *Salpingella* sp. #1 were not enumerated in the gut analysis. Information on the size classes of food available to

Table V. Mean (± standard deviation) abundance (cells l^{-1}) and biomass ($\mu gC\ l^{-1}$) estimates of tintinnid ciliates from Antarctic waters. Biomass has been corrected for the volume to carbon conversion used in this study (Putt & Stoecker 1989) except where noted (*). ($$) denotes abundance estimates of full and empty loricae.

Abundance	Biomass	Remarks	Reference
130±120	0.39±0.39	All tintinnids, all samples	This study
276±169	0.96±0.29	All tintinnids, surface only, open water	This study
72±35	0.86±0.34	*Cymatocylis, Codonellopsis* and	This study
(114±56)$$		*Laackmaniella* only, surface, open water	
100±120	2.46±2.44	Only *Cymatocylis, Codonellopsis*	Boltovskoy *et al.* (1989)
		Laackmaniella and *Coxliella*	
		observed, 62-69°S	
	*110mgC m^{-2}	Predominantly naked ciliates	von Brockel (1981)
	2.1±2.2		Hewes *et al.* (1985)
10		Gerlache Strait	Hopkins (1985)
17		Open water off ice edge	Heinbokel & Coats (1986)
20		McMurdo Bay	Littlepage (1969)
2100		Authur Harbour	Heinbokel & Coats (1985)
3		Weddell/Scotia Sea, winter	Gowing & Garrison (1991)

tintinnids and grazing rates of both tintinnids and their predators is needed to examine further the factors controlling their distribution and the role they play in the microbial food web of the Southern Ocean.

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