Patterns of tintinnine abundance and reproduction near the edge of seasonal pack-ice in the Weddell Sea, November 1983

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ABSTRACT: As part of a study of the ecological dynamics of the Antarctic ice-edge region, we sampled the tintinnine populations at 27 stations in the open water of the Weddell Sea near the edge of the seasonal pack-ice in November 1983. Additional samples were obtained from a second ship operating within the pack-ice. Tintinnine assemblages in the surface water were sparse (≤ 17 individuals l^{-1}) and were primarily composed of the characteristically Antarctic genera *Laackmanniella* and *Cymatocylis*. Tintinnine abundance at the surface was positively correlated with phytoplankton biomass and productivity. Following nuclear staining, epifluorescence microscopy of material collected with vertical net-tows from within the surface mixed layer allowed the determination of the Frequency of Dividing Cells (FDC) for the 2 dominant taxa in these samples. Diel periodicity was not observed in the division of either taxon. FDC for *Laackmanniella* spp. was similar to that previously observed for temperate estuarine tintinnines (40 to 60 %); *Cymatocylis* spp. displayed considerably lower FDC values. FDC for both taxa were unrelated to phytoplankton biomass or productivity. The 2 taxa displayed opposite patterns in the relation between FDC and latitude. *Cymatocylis* spp. had its highest FDC values at the northernmost stations, while FDC of *Laackmanniella* spp. increased with proximity to and beneath the pack-ice. These genera of tintinnines appear to be differentially responding to one or more factors related to latitude, even in the extremely restricted geographic range considered by this study.

INTRODUCTION

The Antarctic pelagic food chain has traditionally been considered to be simple and basically linear: diatoms → krill → carnivores (whales, seals, birds, etc.) (e.g. Everson 1984). Recent data, however, have shown that such simple linear chains in temperate and tropical waters are oversimplifications (e.g. Vinogradov et al. 1973, Greve & Parsons 1977, Landry 1977), perhaps to the degree that an 'unstructured' web of interactions provides a better model of reality (Isaacs 1972, 1973). In particular, recent findings suggest that the 'microplanktonic' (0.02 to 0.2 mm) and 'nanoplanktonic' (0.002 to 0.02 mm) fractions of those temperate and tropical assemblages are generally responsible for the bulk of primary carbon fixation (e.g. McCarthy et al. 1974), nutrient regeneration (Harrison 1980), and respiration (Williams 1982).

Data on abundance and activity of micro- and nano-plankton in Antarctic waters are scarce, but the limited information available suggests that these smaller forms may indeed be significant in the dynamics of the Antarctic planktonic community. Fay (1973) fractionated phytoplanktonic biomass (as chlorophyll) and production (as ^{14}C fixation) by use of a 0.01 mm mesh on a transect through 4 Pacific-Antarctic water masses. More than 60 % of the chlorophyll passed through such a screen. Similarly, 50 to 90 % of the measured primary production was due to the <0.01 mm fraction. Hentschel (1936) found that the Tintinnina (a free-living sub-order of Ciliata) often exceeded 100 individuals l^{-1} in the Weddell Sea. Littlepage (1968) recorded similar densities in McMurdo Sound. According to Brockel (1981) protozooplankton biomass (mainly ciliates) in the euphotic zone averaged 110 (range: 8 to 325) mg C m^{-2} and represented a biomass equivalent to an average of 16 % (range: <1 to 121 %) of the phytoplankton at 24 stations between Bellinghausen Sea and South Georgia. McWhinnie & Denys (1978) experimentally demonstrated that *Euphausia superba* fed omnivorously, thereby supporting the observations of Marr (1962) and Mauchline & Fisher

(1969) that *E. superba* guts contained tintinnines. These observations at least suggest that the Antarctic food-web may not be as simple and linear as classic models have assumed.

Waters near the margin of the seasonal pack-ice appear to be particularly productive in polar regions (e.g. Smith & Nelson 1985). Several mechanisms have been proposed to explain that phenomenon, including (1) physical stabilization of the upper layer of the water column by means of (a) freshwater input from the melting sea-ice or (b) sheltering of the water column from wind mixing; (2) release from the melting sea-ice of 'seed' populations of algae (Smith & Nelson 1985). The Antarctic Marine Ecosystem Research at the Ice-Edge Zone (AMERIEZ) project was initiated to investigate the causes and implications within the food-web of this increased productivity at the seasonal ice-margin in the Weddell Sea. The extent of seasonal pack-ice in the Weddell Sea is extremely variable with the winter edge of the ice extending as much as 1800 km further north than in summer. Average inferred rates of spring dissipation and of autumn formation of this pack-ice are, therefore, on the order of as great as 10 km d^{-1}, although annual and geographical variation and local meterorological events can cause extreme variations around those figures (Mackintosh 1972).

We participated in the first AMERIEZ cruise, 4 Nov to 14 Dec 1983, during late spring dissipation and southward retreat of the ice-edge (Ainley & Sullivan 1984). Our efforts on this cruise had 2 specific objectives: (1) to characterize the diel periodicity (if any) in the cell division cycle of the Tintinnina; (2) to determine how the reproductive dynamics of these ciliates responded to the gradients of phytoplanktonic biomass and productivity expected in the vicinity of the retreating edge of the seasonal pack-ice.

MATERIALS AND METHODS

Study site. Sampling was conducted from 2 research vessels within a defined quadrant of the Weddell Sea (Fig 1). RV *Melville* (Leg 4 of the PROTEA expedition) sampled a grid seaward of the edge of the pack-ice (ca 58° 00' to 60° 40' S. Lat.; 37° 00' to 40° 35' W. Long.), while USCGC *Westwind* sampled a similar grid within the pack-ice (60° 40' to 62° 40' S. Lat.; 36° 25' to 39° 30' W. Long).

Sampling protocols. Sampling of the tintinnine assemblage began aboard RV *Melville* on 10 Nov 1983 with a set of 8 vertical net tows over a 24 h period at Super Station I (ca 60° 33' S. Lat., 37° 5' W. Long.). From 14 to 29 Nov 1983, 24 relatively short (ca 3 to 8 h) stations were sampled with 1 to 3 vertical net tows each. Two additional Super Stations, each consisting of
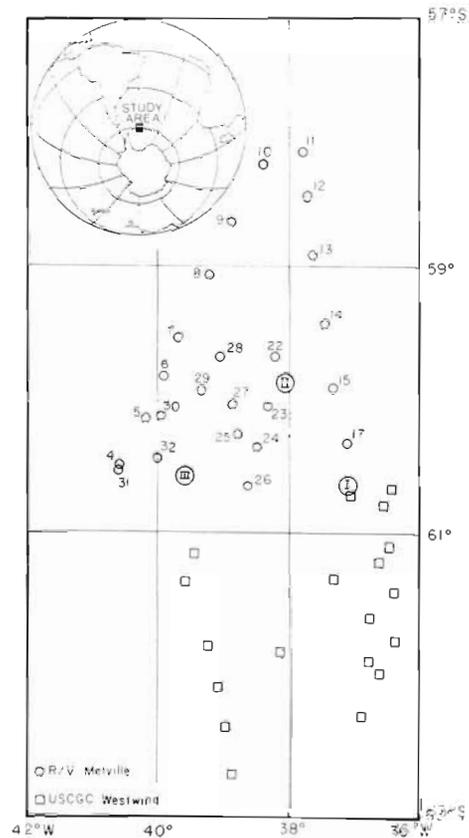

Fig. 1. Location of stations; AMERIEZ, 4 Nov to 14 Dec 1983

12 repeated vertical net tows over 24 h periods were also occupied during that period (Table 1). Each net tow consisted of lowering an open net (30 or 50 cm mouth diameter, 0.035 mm mesh) to 50 m (occasionally other depths when extremely dense or sparse phytoplankton concentrations were anticipated) and raising it slowly (ca 10 to 15 m min^{-1}), through the surface. Particulate material collected in a 500 ml, non-filtering cod-end was gently concentrated further in a secondary filter basket (0.035 mm mesh) to a 100 ml volume. That material was divided into aliquots, each of which was placed into a 22 ml glass scintillation vial. Each of 2 vials was fixed and preserved with 1 ml of $CaCO_3$-buffered formalin, and 1 vial was fixed with an acridine orange/formalin solution (Coats & Heinbokel 1982). Drs. D. L. Garrison and G. Fryxell obtained similar samples for us by vertically towing a 0.035 mm mesh net from 200 m through the surface at stations occupied by USCGC *Westwind*. These latter samples were preserved in glutaraldehyde.

At 20 stations occupied by RV *Melville* an additional sample of surface water was obtained with a clean bucket. Particulate material from 4 l was gently concentrated onto 0.035 mm mesh netting to 20 ml and preserved with basic Lugol's solution. One or more

measured subsamples of that 20 ml was examined by inverted microscopy aboard ship to identify and quantify the tintinnines.

In addition, at each station occupied by RV *Melville* one or more vertical profiles of temperature, conductivity, and *in vivo* fluorescence were made with a CTD; and bottle casts collected water from several depths down to 500 m for analyses of extracted chlorophyll, dissolved nutrients, bacterial abundance and activity, and (during daylight sampling) simulated *in situ* primary productivity. Accoustic systems, several varieties of nets, and an *in situ* camera system sampled the larger zooplankton. Results of these latter studies were reported elsewhere (e. g. Brinton 1984, Fryxell et al. 1984, Garrison et al. 1984, Macaulay et al. 1984, Miller et al. 1984, Nelson et al. 1984, Torres et al. 1984).

Microscopy and analysis. Much of the microscopic examination to define the reproductive dynamics of the net-collected tintinnines was conducted aboard RV *Melville*. Aliquots fixed with the acridine orange/ formalin solution were examined as described by Coats & Heinbokel (1982). Alternatively, 4,6-diamidino-2-phenylindole (DAPI) was added to settling chambers containing sample fixed with $CaCO_3$-buffered formalin. A final concentration of ca 0.5 mg DAPI l^{-1} allowed reasonably clear epifluorescent examination of the nuclear morphology of these ciliates. A Leitz Diavert inverted microscope was used for these examinations; epifluorescent illumination utilized a 100 W mercury burner. For acridine orange-stained materials a Leitz 'H2' filter cube (modified with an auxillary yellow filter) was employed to obtain excitation illumination at 450 to 490 nm with an emission barrier filter allowing passage of light >515 nm.

DAPI-stained samples were examined using a Leitz 'A' filter cube (340 to 380 nm excitation; 430 nm barrier filter). Samples were scanned at 125 to 250 × magnification; 500 × magnification was used, when necessary, to examine individual cells. Both DAPI- and acridine orange-stained samples were examined from

Table 1. Sampling protocols, phytoplankton standing stock (as chlorophyll a concentration), primary production (as carbon fixation rate), and frequencies-of-dividing-cells (FDC) at stations sampled during AMERIEZ cruise aboard RV *Melville*, Nov 1983

Station	Tow depth (m)	No. of tows	Mean chl (mg m^{-3})	Mean I^o product. (mg C m^{-3} h^{-1})	*Laackmanniella* spp. n	FDC	*Cymatocylis* spp. n	FDC
SS–I	75	8	0.30[a]	0.13[a]	558[b]	27 (23–31)[c]	729[b]	10 (8–13)[c]
4	25	1	5.66	1.46	46	20 (9–34)	37	10 (3–25)
5	30	1	3.14	0.54			38	19 (8–35)
6	30	1	4.79	1.00	72	21 (12–32)	52	10 (3–22)
7	30	1	3.98	ND	73	5 (2–14)	45	24 (13–40)
8	30	1	2.04	0.45	32	3 (0–16)	23	35 (16–57)
9	30	1	3.70	ND	28	11 (2–27)	22	23 (8–45)
10	50	1	0.90	0.18				
11	50	1	1.09	ND				
12	30	1	2.87	0.54				
13	30	3	4.23	1.03				
14	50	2	1.63	0.50			69	13 (6–23)
15	50	3	1.21	ND	78	31 (21–43)	228	12 (8–17)
17	50	1	0.88	0.20	20	30 (12–54)	79	12 (5–20)
SS–II	50	12	0.51	0.15			513	17 (14–21)
22	50	1	1.11	0.32				
23	50	2	1.59	0.35			39	3 (0–13)
24	50	3	0.70	0.21			55	9 (3–20)
25	50	1	1.93	0.66				
26	50	1	1.41	ND				
27	50	1	2.54	0.48			21	10 (1–30)
28	50	1	1.45	0.26				
29	50	1	4.95	0.37	31	19 (8–38)		
30	50	1	7.27	0.63			47	6 (1–18)
31	50	1	8.22	0.42				
32	50	1	5.94	0.54				
SS–III	50	12	2.73	0.54	1690	18 (16–20)	2405	6 (5–7)

[a] Chlorophyll (chl) and primary productivity (I^o product.) values are averages from the surface to the depth of the net tow
[b] Number of tintinnines examined
[c] Percent of tintinnies in DNA-synthesis + Division stages of cell cycle (95% confidence limits; Mainland et al. 1956). Blanks denote stations where fewer than 20 cells of that taxa were examined
ND: not determined at this station

Table 2. Tintinnine species list and frequencies of occurrence in surface waters at stations sampled aboard RV *Melville*, Nov 1983

Species	No. of stations
Laackmanniella spp.[a]	12
Cymatocylis spp.[b]	17
Cm. typica	3
Cm. brevicaudata	4
Cm. crassa	1
Cm. parva	2
Cm. cylindroides	2
Cm. flava	5
Cm. vanhoffeni	2
Cm. culcullus	1
Cm. drygalskii	1
Parundella sp.	1
Codenellopsis glacialis	2
Cd. gaussi	2
Cd. sp.	1
Coxliella minor	1
Cx. frigida	2
Bursaopsis quinquealata	1

[a] Consists of *L. naviculaefera* and *L. prolongata*
[b] Consists of *C. convallaria* and *C. scyphus*

RESULTS AND DISCUSSION

Study site

The geographic grid sampled during this cruise was hydrographically complex (D. Mountain & B. A. Huber pers. comm.). Depth of the surface mixed layer ranged over values of 30 to 80 m in open water and increased from 50 m to a maximum of 120 m as the pack-ice was penetrated southward. Surface warming was evident at some open-water stations; only 1 or 2 stations were characterized by a freshened surface layer derived from ice-melt. Water beneath the mixed layer originated from one of several sources: Weddell Sea, Weddell-Scotia Confluence, or Drake's Passage. CTD-derived fluorometry showed a close association of vertical profiles of chlorophyll with the density structure; maximum values were generally found in the lower portion of the mixed layer. Concentrations of chlorophyll at the surface showed a strong east-west gradient, with highest values noted at the south-west corner of the RV *Melville* grid.

Identification and enumeration of tintinnines

Using the monographs of Laackmann (1909) and Kofoid & Campbell (1929), we identified 18 species of tintinnines in our quantitative surface samples from RV *Melville* (Table 2). An additional small *Salpingella* sp. was commonly noted, but not quantified, in net-collected samples from USCGC *Westwind*. Representatives of the characteristically Antarctic genera *Laackmanniella* and *Cymatocylis* were the most common individuals noted.

The maximum observed concentration of tintinnines in these surface samples was 17 individuals l^{-1}, considerably lower than the few previously published enumerations from Antarctic waters. Hentschel (1936), using centrifugation to concentrate his samples, reported tintinnine concentrations in excess of 100 individuals l^{-1} in waters at similar latitudes in the South Atlantic Ocean. Littlepage (1968) reported the presence of 18 tintinnine species in samples collected from McMurdo Sound; densities of tintinnines in his samples were similar to those noted by Hentschel (1936). Our use of 0.035 mm mesh netting to collect tintinnines was based on 2 considerations: our desire to obtain samples comparable to those collected from beneath the pack-ice, and a need to minimize net-clogging and collection of excessive amounts of diatoms and colonial *Phaeocystis pouchetii*. With the exception of the small *Salpingella* sp. noted in the samples taken from beneath the pack-ice, the tintin-

Super Stations I and III and from 3 of the routine stations. Either DAPI- or acridine orange-stained samples were examined from the other routine stations. Samples from all 3 Super Stations and from 13 routine stations were examined aboard RV *Melville*. Samples from the remainder of the routine stations were examined in our laboratory after the cruise. Samples from Super Station III and from several of the routine stations examined at sea were reexamined in our laboratory after the cruise to assess the adequacy of ship-board counts. Glutaraldehyde-fixed samples obtained for us from USCGC *Westwind* were stained with DAPI and examined in our laboratory following the cruise.

Analysis of the reproductive dynamics of the dominant tintinnines closely followed that of Coats & Heinbokel (1982). Based on macro-nuclear morphology, trophic (non-dividing), replication-band (DNA-synthesis), and various post-replication-band (division) stages were distinguished. Since each of the post-replication-band stages was relatively infrequent in our samples, we have pooled them into a single 'division' category for subsequent analyses. Only samples in which we were able to examine at least 20 individuals of a taxa were included in these analyses and the resultant figures presented here (Table 1). With the exception of the Super Stations, the average numbers of cells examined from each station included in these analyses were 48 and 58 for *Laackmanniella* spp. and *Cymatocylis* spp., respectively.

nines we encountered, and those characteristic of the Antarctic in general (Kofoid & Campbell 1929, Hada 1970, Brockel 1981), were sufficiently large that a high percentage of these loricate cells should have been retained by the 0.035 mm mesh. In any case, our estimates of tintinnine abundance must be considered to be minimum values underestimating the true values to the degree that small cells were passing through the concentrating mesh.

Although the number of cells actually enumerated from the surface waters at any one station was low (≤51) and any inferences, therefore, must be considered tentative, tintinnine abundance was positively correlated to both phytoplanktonic biomass (chlorophyll) and productivity (Fig. 2). Calculation of Kendall's *tau*, a non-parametric statistic of correlation (Tate & Clelland 1957) indicated that both relationships were significant ($p < 0.05$).

As in the quantitative surface samples, 2 species each of *Laackmanniella (L. naviculaefera* and *L. prolongata)* and *Cymatocylis (C. scyphus* and *C. convalaria)* dominated the assemblage of tintinnines captured in the net tows. Based on our observations and the discussion of Hada (1970), we have treated the genus *Laackmanniella* as a single entity in our analyses. Similarly we have pooled our data for the 2 dominant *Cymatocylis* species. The validity of the described species, and hence of our treatment of them, could be addressed through modern techniques of staining (e. g. Brownlee 1977, Corliss 1979) but, to our knowledge, these studies have not yet been made.

Reproductive dynamics

Material from the vertical net tows was used to study the reproduction of the dominant taxa of *Laackmanniella* and *Cymatocylis*. Reproduction can be indexed, if not precisely defined, by quantifying the percentage of a protistan population that is in the process of cell division at the time that population is sampled. The optimum sampling strategy for such an effort and the precise analytical procedure will depend largely on the degree to which the population is synchronized over a diel period in its cellular division cycle (Coats & Heinbokel 1982, McDuff & Chisholm 1982). Three Super Stations were repetitively sampled over 24 h periods to determine whether diel periodicity existed in the reproduction of these tintinnine populations.

DAPI- and acridine orange-staining resulted in similar values for the proportion of dividing cells at those stations at which material treated with both stains was examined. DAPI has the advantage that low concentrations of background (not complexed with DNA) stain do not fluoresce, thus eliminating the need to rinse excess stain from the samples prior to examination as is
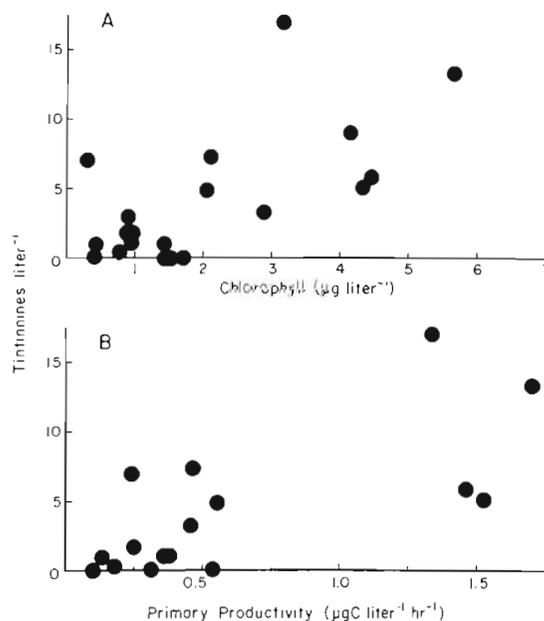

Fig. 2. Concentration of tintinnines in surface water as functions of (A) chlorophyll concentration in surface water; (B) primary productivity in surface water

the case with acridine orange staining (Coats & Heinbokel 1982). Concentration of DAPI in the final preparation, however, is critical, as too low a concentration provides inadequate staining and too high a concentration can lead to a general and obscuring protoplasmic staining, especially in the larger tintinnines such as *Cymatocylis* spp. Ideal concentrations of DAPI should be determined by trial and error for each individual set of samples, a procedure comparable to determining the optimum rinsing time for acridine orange-stained samples (Coats & Heinbokel 1982). In the following discussions no distinction is made between results obtained with DAPI- or acridine orange-staining.

The majority of samples obtained from the 27 stations sampled in this study, including all samples from the Super Stations, were microscopically analysed aboard ship. Vibration from the ship's engines could not be completely eliminated and reduced our microscopic resolution to some degree. On return to our laboratory, we recounted a number of samples from Super Station III to determine if that loss of resolution affected our results. The results for *Cymatocylis* spp., the larger genus characterized by 2 relatively large trophic macronuclei, showed no significant difference between shipboard and laboratory analyses. *Laackmanniella* spp., however, a smaller genus characterized by 4 smaller trophic macronuclei, showed a marked difference between the 2 analyses. The division stages observed were approximately equivalent in the 2 analyses; replication-band stages were consider-
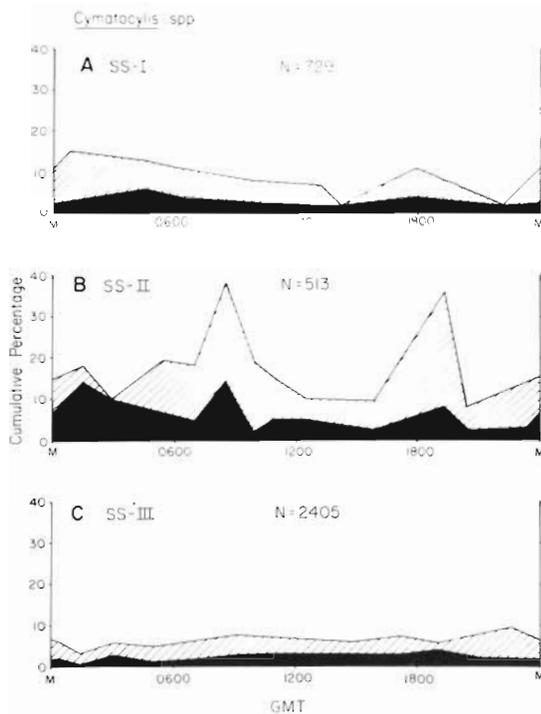
Fig. 3. *Cymatocylis* spp. Cumulative percentages of dividing individuals as a function of time of day. Solid area: division (post-replication band) stages; hatched area: DNA-synthesis (replication-band) stage; N: number of individuals examined. All data are from RV *Melville* Super Stations. (A) Super Station I: 10–11 Nov 1983; (B) Super Station II: 21–22 Nov 1983; (C) Super Station III: 28–29 Nov 1983
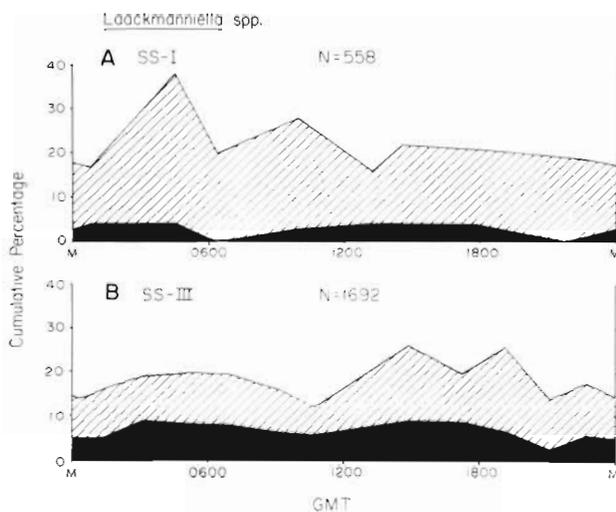

Fig. 4. *Laackmanniella* spp. Cumulative percentages of dividing individuals as a function of time of day. Symbols and dates as for Fig. 2. All data are from ship-board microscopy. (A) Super Station I; (B) Super Station III

ably more numerous in the laboratory analyses, averaging 34 % of the individuals examined vs only 11 % of the individuals examined at sea. Apparently, the relatively subtle early and late portions of this

stage of the cell cycle, during which the replication bands are located near the poles of the macronuclei, could not be reliably discriminated with the reduced microscopic resolution available aboard ship. Accordingly, all data for *Cymatocylis* spp. have been pooled and used in the following analyses and discussions; data derived from shipboard analyses of *Laackmanniella* spp., while internally consistent and thus quite useful for several analyses, have been kept strictly separate from those derived from laboratory analyses.

Results of the repetitive sampling at the Super Stations are presented in Fig. 3 and 4 for *Cymatocylis* spp. and *Laackmanniella* spp., respectively. Although variation is apparent within several of the sampled diel periods, there is nothing that suggests a diel phasing or synchrony in the cell cycle of these 2 tintinnines. This lack of periodicity in the cell cycle is similar to that noted previously for tintinnines in the Chesapeake Bay (Coats & Heinbokel 1982) and has 2 major implications for the analysis of tintinnine specific growth rates. First, a single sample taken at any time of day is likely to accurately characterize the reproduction of that sampled population. Second, an independent measure of the duration of the recognizable division stage(s) will be required to convert the observed frequency-of-dividing-cells (FDC) to a measure of specific growth rate (e.g. McDuff & Chisholm 1982). We do not yet possess any data on the duration of the replication-band or division stages of these Antarctic tintinnines and, therefore, must restrict our subsequent discussion to insights derived from measures of FDC alone.

Observed FDC for *Cymatocylis* spp. and *Laackmanniella* spp. were lower than those observed for tintinnine populations in the Chesaspeake Bay (Coats & Heinbokel 1982). Even winter sampling in the Cheasapeake Bay, when water temperatures ranged from 0 to 5 °C, revealed FDC values of ca 50 % (total of replication-band plus division stages) for 2 tintinnine species; data for *Cymatocylis* spp. and shipboard observations of *Laackmanniella* spp. showed FDC values occasionally at or slightly above 30 % but usually less than 25 %. Reexamination of *Laackmanniella* spp. under vibration-free laboratory conditions, however, suggests that shipboard observations may have underestimated the true FDC of this taxa by at least a factor of 2. In that case, FDC values for *Laackmanniella* spp. would very closely approximate those observed for temperate estuarine species.

The relative frequencies of the replication-band and the division stages for the laboratory-observed *Laackmanniella* spp. were also similar to those noted previously for other populations. In samples from the Chesapeake Bay, replication-band typically exceeds division stages by factors between 5 and 10 (Coats &

Heinbokel 1982). Frequencies of the replication-band stage of *Laackmanniella* spp. exceeded its division stage by a factor of 8.5 (34 vs 4 %), implying, as for the taxa from temperate waters, that the duration of DNA-synthesis greatly exceeds that of division. *Cymatocylis* spp., however, shows a replication-band:division ratio of only 2 (6:3 %), suggesting either a difference in the relative durations of the stages of the cell cycle for this one taxa or a systematic error in our recognition and enumeration of these stages. An underestimate of the replication-band stage or an overestimate of the division stage would lead to such a result. At this time we cannot evaluate these options. However, we would expect any error to be systematic throughout our samples and, therefore, not affect our subsequent analyses of trends and implications of these FDC data.

Geographic variation in FDC

Since there was no evidence of diel periodicity in the FDC data from the 3 Super Stations, we treated the data from each of the 27 stations equivalently, regardless of the time of day at which the sample was taken. For each of the 8 stations at which 2 or more samples were taken (including the Super Stations), all the data were pooled to obtain a single estimate of FDC for that station.

Prior to sampling, our expectation was that phytoplanktonic biomass and productivity would vary in bands parallel to the retreating ice-edge and that any variation in tintinnine reproductive dynamics would be correlated with that phytoplanktonic pattern. Our data and those of others indicate that these expectations were, at best, too simplistic. Chlorophyll a and primary productivity data were provided by W. Smith. Average chlorophyll concentrations in the water column in the depth intervals sampled by our vertical net tows were calculated (Fig. 5; Table 1); the pattern of primary productivity was similar. The observed pattern was more complex than the anticipated simple north-south gradient; considerable east-west variation is also apparent at the southern stations closest to the ice-edge. Stations in the southwest portion of the RV *Melville* sampling grid were characterized by high concentrations of chlorophyll a. Microscopic examination of the surface water from these stations revealed strikingly higher concentrations of *Phaeocystis pouchetii*, a prymnesiophyte forming colonies ≥ 1 mm in diameter within a gelatinous matrix (Stations 6, 7, 29 to 32), and of diatoms *(Thallassiosira gravida)* in a similar gelatinous matrix (Stations 29 to 32) than other stations within the sampling grid. Since these gelatinous colonies are unlikely to be available as food for tintinnines (Spittler 1973, Heinbokel 1978), it is not surprising that the
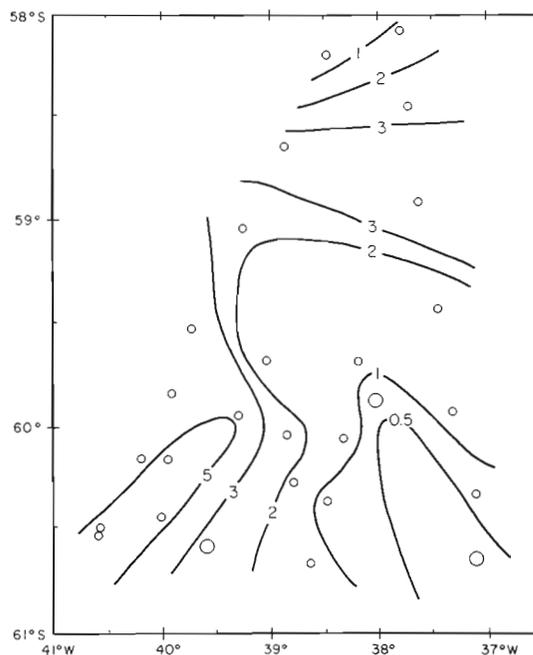

Fig. 5. Chlorophyll distribution for RV *Melville* stations. Data provided by W. Smith (average values, mg chlorophyll m⁻³, calculated for water column to depth of net-tow used to collect tintinnines at each station). Small circles: stations; large circles: Super Stations

observed values of FDC for the 2 dominant tintinnine taxa show no obvious relationship to either chlorophyll a concentration or to rates of primary production (Fig. 6 and 7 respectively; Kendall's *tau* indicated no significant correlation (p > 0.20) for any of the 4 comparisons) within this sampling grid.

We cannot yet explain the apparently contradictory finding that abundance was correlated with the phytoplankton stocks but FDC, an index of reproduction, was not. Several possible explanations can be discussed but all must be considered highly speculative at this time. Perhaps most obviously, the samples used for population enumeration (surface) and FDC analyses (vertically integrating net tows) were not strictly comparable. A second explanation is that, since abundance reflects both growth and mortality, this latter factor (e.g. predation), rather than reproduction, might have been responsible for structuring the tintinnine assemblage. If predatory pressure was related to phytoplanktonic density, such that *per capita* grazing rates were reduced in high concentrations of phytoplankton (e. g. Quetin & Ross 1985), the tintinnines might find an effective refuge in patches of high phytoplanktonic biomass. Finally, since abundance would be the result of growth and mortality acting over some period of time, the history of the various water parcels might also be important. For instance, if high phytoplankton densities characterized water that had been free of

pack-ice for a relatively long period of time allowing the phytoplankton sufficient time to achieve those high densities, then perhaps the tintinnine assemblage had also had a relatively long time in which to grow to its observed density.

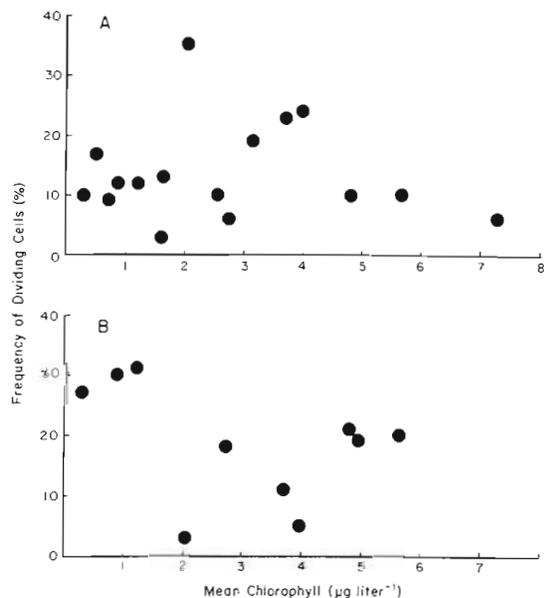Values of FDC for these 2 taxa, however, do display

Fig. 6. Total percentages of dividing tintinnines (both stages) as function of mean chlorophyll concentration as defined in Fig. 5. RV *Melville* stations only. (A) *Cymatocylis* spp.; data from all counts; (B) *Laackmanniella* spp.; data from shipboard only
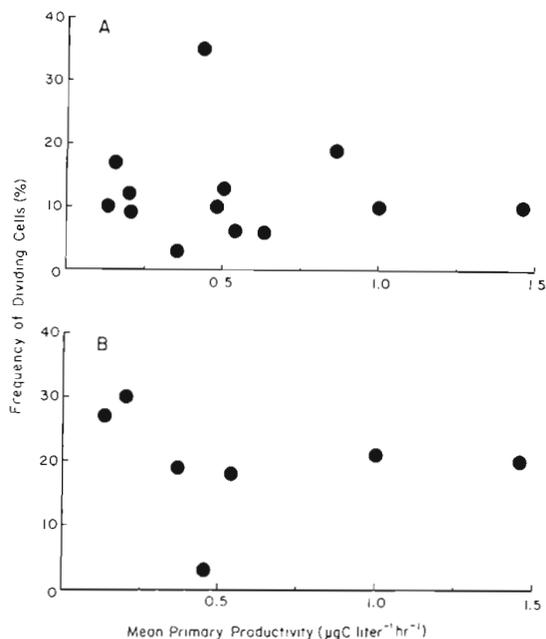
Fig. 7 Total percentages of dividing tintinnines (both stages) as function of mean primary productivity for water column to depth of net-tow used to collect the tintinnines. RV *Melville* stations only. (A) *Cymatocylis* spp.; data from all counts; (B) *Laackmanniella* spp.; data from shipboard only

an inverse relation (Fig. 8), suggesting that *Laackmanniella* spp. and *Cymatocylis* spp. were differentially responding to some environmental factor. When FDC of each of the dominant taxa is plotted as a function of latitude (Fig. 9), the different responses of the 2 taxa are apparent. FDC of *Laackmanniella* spp. tends to increase with increasing latitude, while FDC of *Cymatocylis* spp. is highest at the northernmost stations. Correlation analyses (Kendall's *tau*) indicated that these relationships had significance at the $p < 0.01$ and $0.20 > p > 0.10$ levels for *Cymatocylis* spp. and *Laackmanniella* spp., respectively. While probably itself not of direct importance to the tintinnines, latitude does provide at least a crude index of how recently a given station was overlain by the retreating sea-ice. It appears that *Laackmanniella* spp. attains its maximum FDC at stations closest to and most recently covered by the sea-ice, whereas *Cymatocylis* spp. displays a reduction in FDC at those stations in closest proximity to the ice. This pattern in the data is further strengthened by the results of analysing the samples obtained for us from beneath the pack-ice by D. Garrison and G. Fryxell aboard USCGC *Westwind*. Although quantitative samples were not collected for us, examination of the material collected with the vertical net tows showed a clear numerical dominance of *Laackmanniella* spp. over *Cymatocylis* spp. This pattern is consistent with a scenario in which the *Laackmanniella* spp. population is associated with and is most reproductively active in association with the sea-ice, while *Cymatocylis* spp. shows greater affinity for the more northerly open waters.
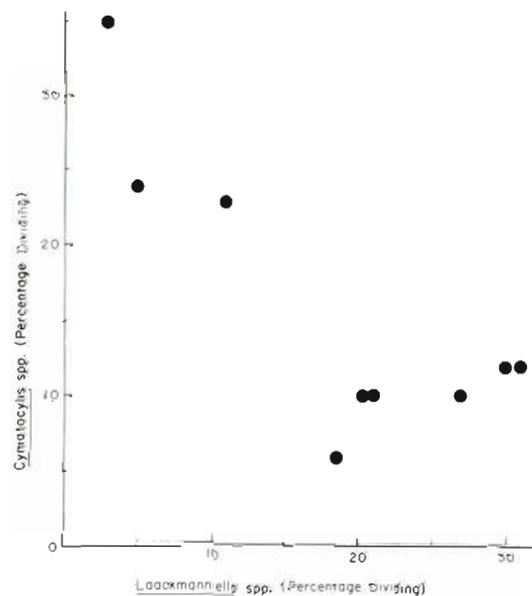

Fig. 8. Total percentage of dividing tintinnines (both stages). *Laackmanniella* spp. data only from shipboard examinations. RV *Melville* stations only
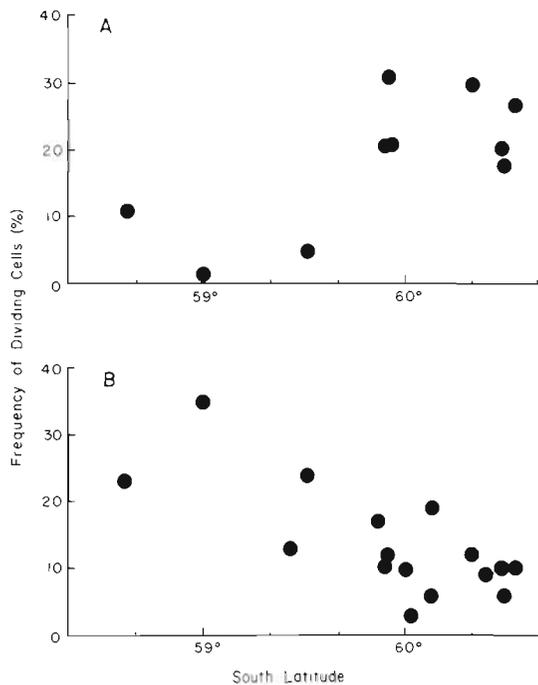
Fig. 9. Total percentage of dividing tintinnines as function of latitude. RV *Melville* stations only. (A) *Laackmanniella* spp.; data from shipboard only; (B) *Cymatocylis* spp.; data from all counts

Laackmanniella spp. displayed a mean FDC of 37 % (33 % replication-band; 4 % division) in samples obtained from beneath the pack-ice by USCGC *Westwind*. Since these data were derived from laboratory examinations of samples, they are not strictly comparable to the ship-board examinations reported and discussed previously. When compared to the stations sampled by RV *Melville* for which laboratory enumerations are available, however, it is clear that values of
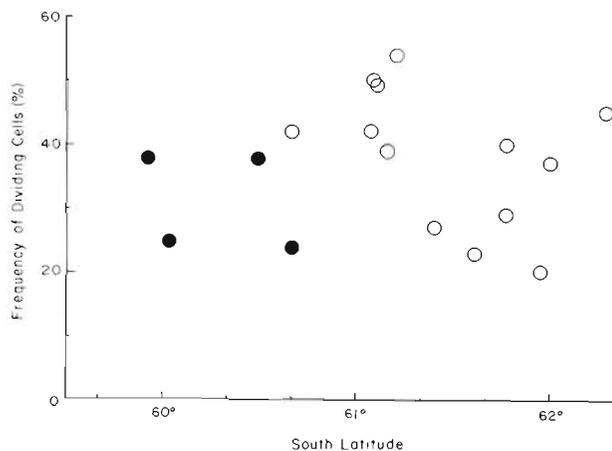

Fig. 10. *Laackmaniella* spp. Laboratory determinations of total percentages of dividing cells as function of latitude. Closed circles: data from RV *Melville* samples; open circles: data from USCGC *Westwind* samples

FDC for populations of *Laackmanniella* spp. beneath the ice are very similar to those from those open water stations closest to the ice (Fig. 10). Although the precise abundance of this population of tintinnines beneath the ice is uncertain, it is actively reproducing and is characterized by values of FDC very similar to the maximum values noted for populations in the open water just north of the pack-ice. Only 50 individuals of *Cymatocylis* spp. were noted in all the samples from beneath the pack-ice; the pooled data from those stations resulted in a FDC of 16 %, all in the replication-band stage.

Although we do not yet have the information on the duration of recognizable division stages required to convert FDC to specific growth rates, our data are sufficient for several conclusions. Tintinnine ciliates were present in the surface waters of the Weddell Sea near and beneath the retreating seasonal pack-ice in spring 1983. Although the diversity of tintinnines was relatively low (cf. Heinbokel & Beers 1979) and their total abundance less than previous reports (Hentschel 1936, Littlepage 1968), the abundance of tintinnines in surface waters was positively correlated to biomass and productivity of the phytoplankton. The dominant taxa of tintinnines in that region were reproducing; and one genus, *Laackmanniella* spp., was characterized by FDC values similar to those previously observed for temperate populations of tintinnines. No diel periodicity in cell division was observed. FDC, unlike abundance, showed no relationship to abundance or productivity of the phytoplankton. Trends in FDC of the two dominant taxa were inversely related and appeared to vary with latitude, suggesting different origins or adaptations for those taxa. *Laackmanniella* spp. appears to be closely associated with the seasonal pack-ice, while *Cymatocylis* spp. is more abundant and is characterized by higher values of FDC in the open water north of the ice-edge.

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