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Ciliates and heterotrophic dinoflagellates in the marginal ice zone of the central Barents Sea during spring

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Diversity and biomass of ciliates and heterotrophic dinoflagellates were analysed at six stations on a south–north transect (mimicking a time span of months in the biological succession during the Arctic spring–summer) from open water through drift ice and into fast ice (72°30′N 76°32′N) during spring 1993 in the open Barents Sea. A pycnocline was observed beneath the sea ice at 40–50 m. A diatom spring bloom beneath the ice with chlorophyll-*a* maximum $>10\,\mu g\ l^{-1}$ and a diverse protozoan community with a peak biomass of $34\,\mu g\ C\ l^{-1}$ was associated with this bloom. Maximum biomass of tintinnids ($1\,\mu g\ C\ l^{-1}$), athecate dinoflagellates ($8\,\mu g\ C\ l^{-1}$) and thecate dinoflagellates ($26\,\mu g\ C\ l^{-1}$) were found associated with the chlorophyll-*a* maximum in the upper 10 m of the water column beneath the sea ice at the northern stations. In contrast, the protozooplankton community was dominated by naked ciliates at the southern open water stations. Here chlorophyll-*a* was low ($<1\,\mu g\ l^{-1}$) and the maximum biomass of protozooplankton was $10\,\mu g\ C\ l^{-1}$ of which naked ciliates accounted for $>50\%$.

Cell sizes and estimated carbon content of cells $>11\,\mu m$, as well as depth by depth biomass of 12 species/types of naked ciliates, 12 tintinnids, 12 athecate dinoflagellates and 24 thecate dinoflagellates, are presented. The community of naked ciliates was dominated by *Strombidium* spp. and *Strobilidium* spp., the tintinnids were dominated by *Parafavella* spp., *Ptychocylis*, *Leprotintinnus*, *Acanthostomella* and *Tintinnopsis*. The very small gyro-/gymnodinoid cells and *Gyrodinium* cf. *spirale* dominated the athecate dinoflagellates and the thecate dinoflagellates by the heterotroph *Protoperidinium* spp. generally accounted for the major part of the protozooplankton biomass along the transect. The Margalef diversity index revealed lowest diversity of ciliates and heterotrophic dinoflagellates in the open water and higher at ice-associated stations. The overall diversity was coupled with prey availability in terms of food concentration, but already saturated at $0.1\,\mu g$ chlorophyll-$a\ l^{-1}$.

INTRODUCTION

During the last two decades it has been increasingly evident that protozoans play a significant role in the pelagic food web linking primary production and production at higher trophic levels (Smetacek, 1981; Hansen, 1991; Bralewska & Witek, 1995). Protozooplankton cover several predatory niches and are potential grazers of bacteria, nanoflagellates, protozoa, phytoplankton and even copepod eggs. Protozooplankton links further within the pelagic food web as potential prey for metazoan zooplankton and fish larvae (Sherr et al., 1986; Stoecker & Capuzzo, 1990).

Two major components of protozooplankton, the ciliates and the heterotrophic dinoflagellates, have been shown to play different functional roles. Heterotrophic dinoflagellates are often observed during or just after spring blooms of diatoms in coastal waters (Hansen, 1991; Lessard, 1991), whereas the ciliate component is often more pronounced in the open sea or during the summer, characterized by small-celled phytoplankton (Hansen, 1991; Nielsen & Kiørboe, 1994). However, many basic questions such as taxonomy, life cycles and succession patterns, and functional questions like feeding preferences and energy budgets of individual species still remain unanswered and require further investigation (Bralewska & Witek, 1995).

It has been shown that absolute abundance of ciliates and heterotrophic dinoflagellates in the boreal Pacific, western Arctic and Antarctic waters were as high as those found in temperate waters (Sorokin, 1977; Heinbokel & Beers, 1979; Smetacek, 1981; Paranjape, 1987; Levinsen et al., 1999). However, not much is known about the quantitative importance of ciliates and heterotrophic dinoflagellates from polar regions (Paranjabe, 1988; Hansen et al., 1996; Levinsen et al., 1999), and only sporadic or superficial descriptions of the protozooplankton diversity, succession and biomass are available from the Barents Sea (Wulff, 1919; Dale, 1986; Hansen et al., 1996). It is hypothesized that the taxonomic composition of the major protozooplankton components follows the trophic status of a given water mass rather than a traditional zoogeographical distribution pattern (Stoecker et al., 1994). Typically, larger species of ciliates and dinoflagellates are prevalent during spring while smaller species dominate during summer (Montagnes et al., 1988; Hansen, 1991).

The aim of this study was to describe the diversity in detail, and estimate the quantitative appearance of the different ciliate and heterotrophic dinoflagellate taxons during the spring bloom in the central Barents Sea. This includes the relative distribution across the marginal ice zone from open Atlantic waters into Polar waters with the goal of analysing possible distribution factors for these organisms.

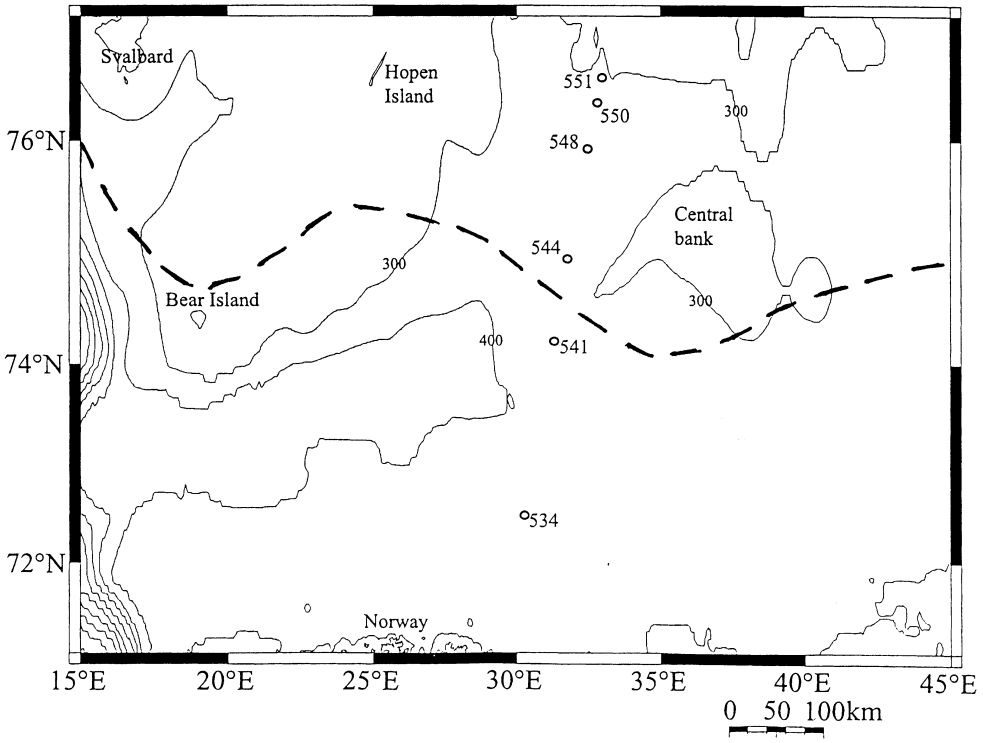

Figure 1. Map of the Barents Sea with stations: 534, 72°30′N 30°14′E; 541, 74°13′N 31°16′E; 544, 74°58′N 31°42′E; 548, 75°56′N 32°24′E; 550, 76°22′N 32°45′E; 551, 76°32′N 32°55′E. Dotted line, average position of the border for close drift ice during the investigation period.

MATERIALS AND METHODS

During a cruise with RV 'Jan Mayen', University of Tromsø, from 12 to 29 May 1993, a plankton study was performed covering a south–north transect roughly along 30°E from 72°30′N to 76°32′N. The transect crossing the Polar Front included six sampling stations of which one was positioned in open water, two in drift ice, one in close drift ice and two were positioned in fast sea ice (Figure 1).

The sampling programme included Neal Brown conductivity, temperature and density (CTD) and fluorometry profiles. Water samples were taken with 10-l Niskin water bottles in 6–9 discrete depths covering the productive water strata down to 100 m depth. Phytoplankton biomass was described by chlorophyll-*a* concentrations by filtering water samples onto GF/C filters, which were extracted in methanol, and measured on a Turner Designs fluorometer (Strickland & Parsons, 1972).

Protozooplankton (ciliates and heterotrophic dinoflagellates) $>11\,\mu$m equivalent spherical diameter were subsampled from whole water samples in 200–300 ml bottles and immediately fixed with 1% final concentration of acid Lugol's solution. The samples were kept in the dark in a 5°C cold room until analysis. After sedimentation of 11 μm screened samples in 25 ml sedimentation chambers ciliates and heterotrophic dinoflagellates were identified to the lowest possible taxonomic group using an inverted microscope (Nikon Diaphot 300) at a magnification of ×200–400. Species identification was performed using general morphology, size, ciliature etc., by consulting the following literature: naked ciliates (Maeda, 1986; Maeda & Carey, 1985), tintinnids (Marshall, 1969), dinoflagellates (Drebes, 1974; Tomas, 1996). The fixative made it impossible to differentiate between heterotrophic, mixotrophic or autotrophic taxa. All ciliates were considered to be heterotrophic. It is known that *Myrionecta* (*Mesodinium*) *rubra* is an obligate autotroph (Lindholm, 1985), but as it only made up a minor part of the biomass it was not eliminated from the results.

All athecate dinoflagellates were assumed to be heterotrophic although some of the species in our list possibly are autotrophic (*Torodinium robustum*, some of the *Amphidinium* spp.) and *Gyrodinium* (e.g. *G.* cf. *aureolum*, *G.* cf. *pulchellum*, *G.* cf. *longum*, *Gyrodinium* (*Sclerodinium*) *calyptroglyphe*). The largest portion of the athecate dinoflagellates belonged to gyro-/gymnodinoide species that could not be identified to species and the contribution of autotrophy or mixotrophy could not be evaluated by this method. Some of the thecate dinoflagellates are also known to be autotrophic (e.g. *Ceratium*, *Protoceratium*, *Prorocentrum*, *Gonyaulax*, *Dinophysis acuta*, *Dinophysis norvegica*), but their overall contribution to total biomass was below 1%. No attempt was made to correct for cell shrinkage due to fixation or loss due to storage of samples. The linear dimensions of cells were measured at each station and depth (N=10 individuals of each species per sample) and the plasma volume calculated from geometrical forms. The carbon content was calculated assuming a carbon to plasma volume ratio of 0.13 pg C μm^{-3} for thecate dinoflagellates and 0.11 pg C μm^{-3} for other taxonomic groups (Edler, 1979). To give the necessary thorough description of all important taxa found (N=61 taxa) the average cell length, cell width, plasma volume and carbon content were calculated (N=27–694 specimens for each species) for all species at all sampling

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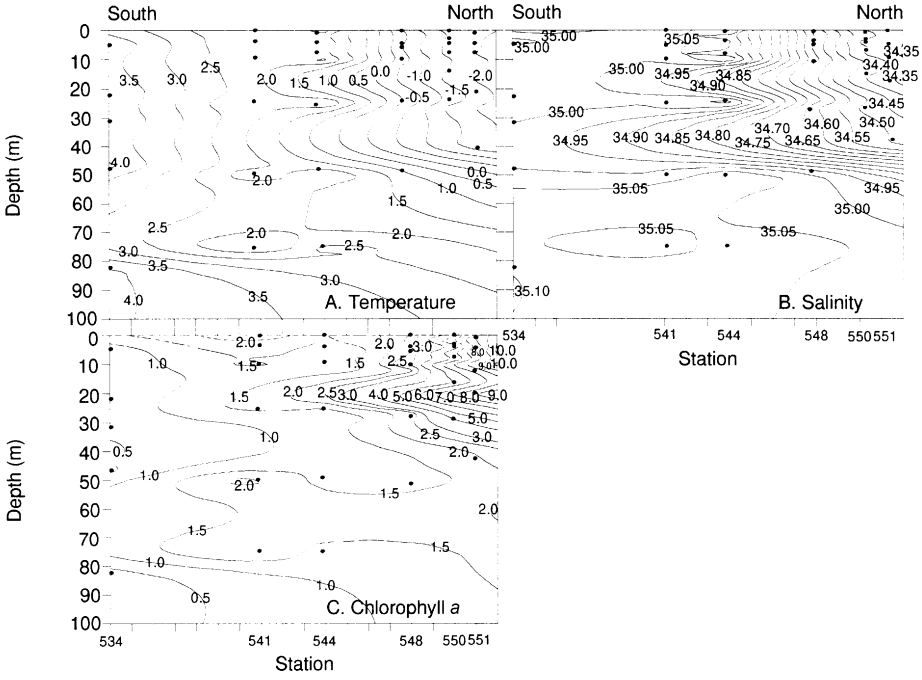

Figure 2. Isopleth diagrams of (A) water temperature (°C), (B) salinity (psu), and (C) chlorophyll-*a* (μg l^{-1}) along a south–north transect in the central Barents Sea during spring 1993.

stations and are given in Table 1. No systematic differences in cell sizes between stations or water depths were found and these were not essentially different to values found in literature.

An analysis of ciliate and heterotrophic dinoflagellate diversity as a mean ±SE for all water depths and at 5 m at each station along the transect were performed according to Margalef (1997): k=log S/log N, where S=number of taxons and N=number of individuals. Additionally, the k-values were related to food availability (chlorophyll-*a*) by Michaelis–Menten kinetics [k= (chlorophyll-*a*) $\times K_{max}/$(chlorophyll-*a*)$+K_m$] and to water depth by a linear fit (SigmaPlot, Jandel Scientific). For determining distribution of individual species of protozooplankton, a Canonical Analysis (Statistica, StatSoft) was performed in order to quantify forcing functions (water depth, temperature, salinity, chlorophyll-*a*) by a multivariate correlation tool.

RESULTS

A pycnocline at 40–50 m depth beneath the ice-surface was observed at the northern site (Figure 2A,B). Water temperature was uniform at 3–4°C and 2°C through the water column in the south of the transect at stations 534 and 541, respectively, and declined below zero towards the north (stations 550, 551). Salinity dropped in the upper 40 m along the transect from 35 to 34.45 psu along the transect due to dilution from the melting sea ice. The chlorophyll-*a* concentration was approximately 0.5–1 μg l^{-1} and uniformly distributed throughout the water column in the south and increased especially above the pycnocline towards the north along the transect (Figure 2C). Beneath the sea ice covered stations in the northern section of the transect, a chlorophyll-*a* maximum of approximately 10 μg l^{-1} was measured in the upper 10 m of the water

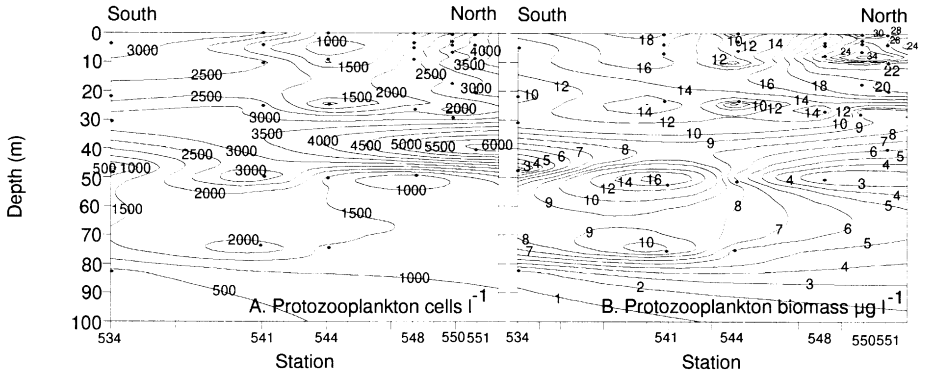

Figure 3. Isopleth diagrams of (A) protozooplankton, ciliates and heterotrophic dinoflagellates, abundance (cells l^{-1}) and (B) biomass (μg C l^{-1}) along a south–north transect in the central Barents Sea during spring 1993.

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Table 1. *Calculated means ±SD of cell length, width, plasma volume and biomass for taxonomic groups in the central Barents Sea during spring 1993.*

	N	Length mean ±SD (μm)	Length range min	Length range max	Width mean ±SD (μm)	Width range min	Width range max	Volume mean ±SD (μm³)	Volume range min	Volume range max	Biomass mean ±SD (pg C)	Biomass range min	Biomass range max
Naked ciliates													
Strombidium cf. *wulffi*	180	63.7 ±10.9	30	95	38.9 ±6.8	25	60	39,771 ±16,962	7,366	106,071	4,375 ±1,866	810	11,668
Strombidium cf. *pulchrum*	119	126.0 ±25.0	75	200	52.2 ±9.1	30	95	97,515 ±55,709	18,857	425,464	10,727 ±6,128	2,074	46,801
Strombidium spp.	694	40.7 ±16.8	15	150	28.8 ±8.5	15	95	16,968 ±21,910	1,414	298,031	1,866 ±2,410	156	32,783
Laboea strobila	90	102.5 ±18.2	60	150	53.5 ±7.6	30	90	80,348 ±33,310	14,143	212,143	8,838 ±3,664	1,556	23,336
Lohmaniella oviformis	358	21.5 ±3.6	12	32	19.3 ±4.1	12	35	4,263 ±2,931	905	22,458	469 ±322	100	2,470
Strobilidium cf. *spiralis*	208	81.7 ±17.1	50	160	60.3 ±12.5	30	85	129,275 ±72,938	14,143	321,685	14,220 ±8,023	1,556	35,385
Strobilidium sp. (cone-shaped)	46	78.2 ±13.3	50	110	49.0 ±5.4	40	65	49,501 ±14,057	26,796	110,655	5,445 ±1,546	2,948	12,172
Strobilidium spp.	111	54.9 ±22.0	25	115	44.0 ±17.0	18	100	66,774 ±91,467	3,055	523,81	7,345 ±10,061	336	57,619
Myrionecta cf. *rubrum*	165	35.8 ±8.4	17	65	29.4 ±8.4	15	70	19,674 ±18,749	2,004	154,000	2,164 ±2,062	220	16,940
Scuticuciliata	303	38.8 ±6.0	20	62	21.0 ±4.3	12	40	5,641 ±3,309	880	24,444	621 ±364	97	2,689
Tintinnids													
Tintinnopsis spp.	87	52.7 ±30.0	25	240	35.6 ±9.1	20	51	21,541 ±22,111	2,724	163,491	2,370 ±2,432	300	17,984
Leprotintinnus pellucidus	25	59.3 ±14.0	35	88	26.0 ±2.8	20	32	21,181 ±6,042	8,873	28,81	2,330 ±665	976	3,169
Parafavella gigantea	137	86.8 ±16.1	42	115	42.4 ±6.1	26	95	84,309 ±39,222	31,869	449,101	9,274 ±4,314	3,506	49,401
Ptychocylis acuta	28	68.6 ±9.8	50	90	46.6 ±5.4	25	55	79,200 ±21,000	26,191	118,839	8,712 ±2,310	2,881	13,072
Athecate dinoflagellates													
Gyrodinium cf. *spirale*	469	67.1 ±18.2	31	130	27.4 ±7.8	15	70	16,117 ±15,865	2,063	154,000	1,773 ±1,745	227	16,940
Gyrodinium cf. *longum*	51	78.4 ±28.1	34	155	26.2 ±9.1	10	50	37,395 ±36,784	1,886	183,333	4,114 ±4,046	207	20,167
Gyrodinium cf. *dominans*	428	27.7 ±6.1	11	50	18.8 ±4.3	8	35	5,876 ±3,906	469	28,875	646 ±430	52	3,176
Gyrodinium cf. *calyptoglyphe*	100	29.4 ±5.2	20	45	22.7 ±4.7	15	38	6,932 ±4,925	1,768	28,743	763 ±542	195	3,162
Gyrodinium cf. *pulchellum*	102	21.2 ±2.6	17	30	19.3 ±2.7	14	26	3,999 ±1,731	1,437	9,207	440 ±191	158	1,013
Gyrodinium cf. *aureolum*	66	26.4 ±3.9	18	40	24.1 ±3.8	17	40	7,883 ±4,379	2,574	33,524	867 ±482	283	3,688
Katodinium glaucum	283	32.7 ±6.1	20	55	15.5 ±2.6	9	26	4,383 ±2,287	849	16,369	482 ±252	93	1,801
Torodinium robustum	181	46.0 ±10.5	26	77	21.6 ±4.1	12	37	7,902 ±3,696	1,307	19,123	869 ±407	144	2,104
Amphidinium sphenoides	186	47.3 ±11.7	25	80	15.9 ±3.8	9	30	3,669 ±2,955	552	18,857	404 ±325	61	2,074
Cochlodinium sp.	79	30.7 ±10.0	16	80	20.6 ±4.6	10	33	7,575 ±5,167	838	26,810	833 ±568	92	2,949
Thecate dinoflagellates													
Protoperidinium bipes	138	41.2 ±5.5	29	55	29.8 ±4.2	20	40	14,623 ±6,045	4,191	33,524	1,901 ±786	545	4,358
Protoperidinium depressum	349	154.2 ±13.6	115	198	138.2 ±13.0	100	175	588,427 ±142,868	255,36	1,094,844	76,496 ±18,573	33,196	142,330
Protoperidinium pellucidum	229	52.0 ±5.8	35	65	52.8 ±6.8	27	70	80,770 ±29,142	10,31	179,666	10,500 ±3,789	1,340	23,357
Protoperidinium pallidum	57	86.5 ±13.5	62	110	78.8 ±13.1	52	108	277,287 ±142,813	73,652	659,849	36,047 ±18,566	9,575	85,780
Protoperidinium steinii	27	49.9 ±8.3	37	65	42.2 ±7.1	31	55	42,437 ±20,734	15,605	87,149	5,517 ±2,695	2,029	11,329
Protoperidinium islandicum	55	66.0 ±13.5	45	110	82.5 ±7.8	65	100	171,043 ±125,106	47,732	697,191	22,236 ±16,264	6,205	90,635
Protoperidinium cf. *brevipes*	70	35.1 ±9.2	20	60	38.1 ±9.2	24	60	27,547 ±22,620	4,191	113,143	3,581 ±2,941	545	14,709
Protoperidinium cf. *granii*	43	54.3 ±9.2	35	69	57.0 ±5.3	48	65	99,492 ±27,425	57,929	143,851	12,934 ±3,565	7,531	18,701
Diplopsalis-group, unidentified	144	55.9 ±13.3	25	85	62.9 ±14.5	25	95	107,215 ±71,467	8,185	321,685	13,938 ±9,291	1,064	41,819
Dinophysis acuta	66	65.1 ±5.6	55	75	48.1 ±4.3	37	58	39,841 ±8,469	24,023	65,198	5,179 ±1,101	3,123	8,476
Dinophysis rotundata	27	53.9 ±5.4	40	65	46.2 ±5.3	33	53	72,346 ±20,122	26,620	102,997	9,405 ±2,616	3,461	13,390
Ceratium fusus	41	458.5 ±97.2	135	720	35.0 ±10.4	21	60	28,527 ±26,069	4,851	113,143	3,709 ±3,389	631	14,709

N, number of measured organism; min, minimum; max, maximum.

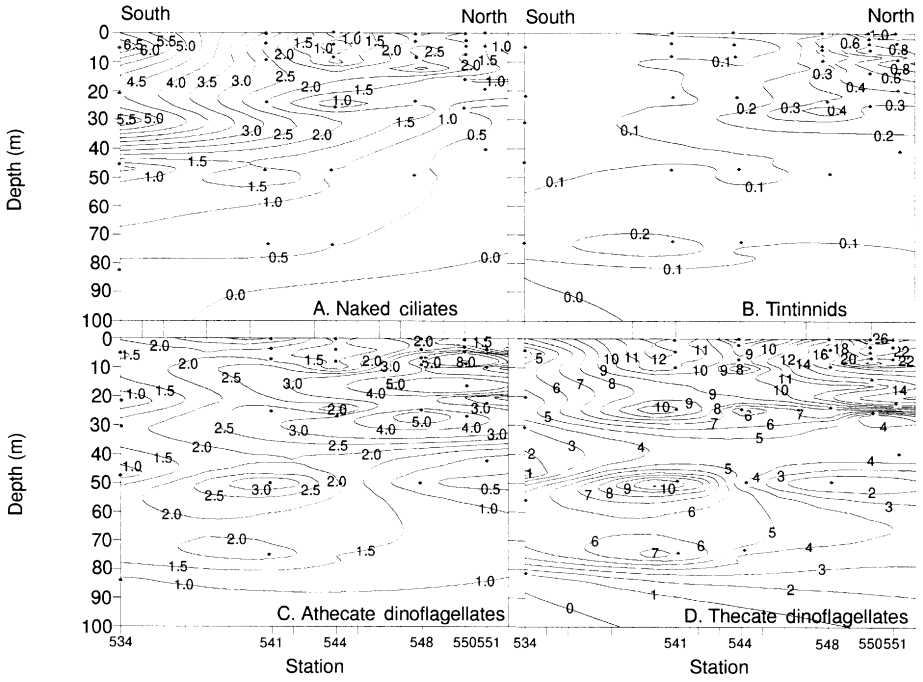

Figure 4. Isopleth diagrams of biomass (μg C l^{-1}) of (A) naked ciliates, (B) tintinnids, (C) athecate dinoflagellates, and (D) thecate dinoflagellates along a south–north transect in the central Barents Sea during spring 1993.

column. The chlorophyll-*a* maximum consisted mostly of chain-forming diatoms (*Thalassiosira* spp., *Chaetoceros* spp.).

Biomass of naked ciliates (Table 2) was dominated by *Strombidium* spp. and *Strobilidium* spp. and consisted of a wide range of forms that could not be identified to species mainly due to lack of accurate descriptions in the literature.

Tintinnids (Figure 4B, Table 2) never formed a major part of the biomass, and were mainly dominated by species from the genus *Parafavella* (especially *P. gigantea*), which were most diverse beneath the ice. *Parafavella cylindricus*, *P. denticulata*, *P.* cf. *parundata*, *P.* cf. *elegans*, *P.* cf. *robustum*, *P.* cf. *dilatata*, *P.* cf. *edentata* were observed along the entire transect, but at low densities.

Athecate dinoflagellate biomass consisted mainly of unidentifiable small gyro-/gymnodinoide cells (Table 2), but among those identifiable *Gyrodinium* cf. *spirale* was the dominant taxon present at all stations along the transect.

Thecate dinoflagellates were present as a very diverse community especially beneath the sea ice at station 550 and station 551 (Figure 4D). A range of species belonging to the genus *Protoperidinium* were identified and *P. depressum* was the main contributor to both the thecate dinoflagellate and to the overall protozooplankton biomass at all sampling stations (Table 2). *Protoperidinium bipes*, *P. pellucidum*, *P. pallidum*, *P. pyriforme*, *P. oblongum*, *P. steinii*, *P. thorianum* were abundant and one or few cells of *P.* cf. *claudicans*, *P.* cf. *excentricum*, *P.* cf. *conicum*, *P.* cf. *leonis*, *P.* cf. *ovatum*, *P.* cf. *curvipes*, *P.* cf. *atlanticum* were found. The autotrophic *Prorocentrum* was found at the southernmost station where the chlorophyll-*a* concentration was low, whereas the autotrophic *Gonyaulax* and *Protoceratium* were only found at the northernmost station where the chlorophyll-*a* concentration was high, but none of them contributed significantly to the biomass.

Thecate dinoflagellates made up the largest part of the protozooplankton biomass, reaching 26 μg C l^{-1} beneath the sea ice (Figure 4D). The athecate dinoflagellates and the tintinnid biomass followed the chlorophyll-*a* concentration, but only reached 8 μg C l^{-1} and 1 μg C l^{-1}, respectively (Figure 4B,C). In contrast, the naked ciliate biomass reached a maximum of 6.5 μg C l^{-1} in the upper 30 m of the water column in the southern section of the transect (Figure 4A).

No significant overall positive correlation was observed between ciliate and heterotrophic dinoflagellate abundance and biomass vs the abiotic factors as well as chlorophyll-*a*. In terms of abundance, the highest protozooplankton concentration was found at 40–50 m depth beneath the ice due to the presence of many small athecate dinoflagellates, mainly gyro-/gymnodinoids (Figure 4C). However, protozooplankton biomass tended to follow the chlorophyll-*a* reaching a maximum of approximately 34 μg C l^{-1} in the upper 10 m of the water column beneath the ice at the northern stations (Figure 3B). Biomass and diversity declined southwards and with depth in the water column (Figures 3B & 5D).

Both the mean k (Margalef diversity index) for all water depths and the k for 5m depth revealed that the ciliate and heterotrophic dinoflagellate diversity was lowest in the open water and higher in ice-associated stations (Figure 5A,B). The community composition was coupled to prey availability in terms of phytoplankton concentration (Figure 5C). However, the half saturation constant km was as low as 0.05 μg chlorophyll-*a* l^{-1} (Figure 5C). According to the Canonical Analysis in particular the abundance of single species like *Protoperidinium depressum* and *Parafavella gigantea* were governed by chlorophyll-*a*. The abundance of the *Diplopsalis*-group, *Alexandrium* sp., *P. gigantea* and *Lohmaniella oviformis* were significantly inversely related to temperature and salinity (Table 3).

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Table 2. *Integrated (0–100 m) biomass (mg C m^{-2}) of taxonomic groups at the sampling stations in the central Barents Sea during spring 1993.*

		Station					
Taxon	(mg m^{-2})	534	541	544	548	550	551
Naked ciliates							
Strombidium spp.		0.1866	0.0650	0.0038	0.0448	0.0163	0.0302
Laboea strobila		0.0014	0.0178	0.0016	0.0010	0.0005	0.0061
Strombidinopsis cf. *spinifera*		–	0.0001	0.0005	0.0003	–	–
Strombidinopsis sp.		0.0000	0.0002	0.0002	–	–	0.0000
Lohmaniella oviformis		0.0000	0.0004	0.0001	0.0002	0.0001	0.0004
Strobilidium spp.		0.0131	0.0695	0.0411	0.0795	0.0243	0.0072
Myrionecta cf. *rubra*		0.0420	0.0076	0.0021	0.0029	0.0029	0.0029
Askenasia sp.		–	–	–	–	0.0001	0.0000
Scuticuciliata		–	0.0088	0.0003	0.0082	0.0018	0.0003
Prorodontida		–	0.0005	0.0011	0.0007	0.0003	0.0002
Hypotrichia		0.0057	–	–	–	–	–
Unidentified ciliates		–	–	–	0.0008	0.0040	0.0026
total	(mg m^{-2})	0.2489	0.1698	0.0507	0.1383	0.0503	0.0503
Tintinnids							
Tintinnopsis spp.		0.0003	–	0.0001	0.0099	0.0069	–
Leprotintinnus spp.		–	0.0006	0.0001	0.0012	0.0002	0.0002
Parafavella gigantea		–	–	0.0002	0.0043	0.0115	0.0214
Parafavella denticulata		–	–	0.0002	–	–	0.0022
Parafavella spp.		–	0.0071	0.0005	–	0.0002	0.0005
Achantostomella norvegica		–	0.0001	0.0018	–	–	0.0001
Ptychocylis acuta		–	–	–	0.0105	0.0103	0.0011
Ptychocylis obtusa		–	0.0131	0.0014	–	–	–
Ptychocylis sp.		–	–	0.0002	–	–	–
Salpingella secata		0.0003	–	0.0003	–	0.0018	0.0005
Salpingella cf. *ungiculata*		0.0000	–	–	–	–	–
Stenostomella cf. *oliva*		–	–	–	–	–	0.0000
total	(mg m^{-2})	0.0005	0.0208	0.0047	0.0259	0.0308	0.0261
Athecate dinoflagellates							
Gyrodinium cf. *spirale*		0.0032	0.2402	0.0124	0.0166	0.0071	0.0183
Gyrodinium cf. *dominans*		–	0.0113	0.0122	0.0088	0.0014	0.0003
Gyrodinium cf. *calyptroglyphe*		0.0004	–	–	–	0.0032	0.0055
Gyrodinium cf. *pulchellum*		–	–	–	–	–	0.0062
Gyrodinium cf. *longum*		–	–	–	0.0025	0.2965	0.0027
Gyrodinium cf. *aureolum*		0.0000	–	–	–	0.0024	0.0024
Katodinium glaucum		0.0001	0.0020	0.0014	0.0016	0.0041	0.0033
Amphidinium sphenoides		–	0.0020	0.0012	0.0023	0.0025	0.0006
Amphidinium spp.		0.0002	–	0.0000	–	0.0001	0.0003
Torodinium robustum		0.0004	0.0024	0.0035	0.0017	0.0020	0.0052
Cochlodinium spp.		–	–	0.0130	0.0007	0.0026	0.0012
Unidentified athecate							
Dinoflagellates		0.0905	0.2899	0.1042	0.1844	0.2079	0.0669
total	(mg m^{-2})	0.0947	0.5478	0.1478	0.2185	0.5299	0.1130
Thecate dinoflagellates							
Protoperidinium depressum		0.1076	0.7247	0.3278	0.2968	0.3023	0.6201
Protoperidinium bipes		–	0.0271	0.0023	0.0083	0.0077	0.0140
Protoperidinium pellucidum		0.0150	0.1130	0.0191	0.0363	0.0635	0.0679
Protoperidinium pallidum		–	0.0556	0.0250	0.0110	0.0354	0.0274
Protoperidinium pyriforme		0.0028	0.0002	0.0012	–	–	0.0009
Protoperidinium oblongum		–	0.0012	0.0135	0.0016	0.0002	0.0010
Protoperidinium islandicum		–	0.0018	0.0044	0.0219	0.0025	0.0005
Protoperidinium brevipes		–	0.0027	0.0026	0.0050	0.0095	0.0003
Protoperidinium steinii		–	–	0.0006	0.0050	0.0111	0.0052
Protoperidinium thorianum		–	–	–	0.0104	0.0151	–
Protoperidinium spp.		0.0028	0.1464	0.0112	0.0144	0.0272	0.0056
Diplopsalis-group,unidentified		0.0097	–	0.0025	0.0458	0.0153	0.0583
Alexandrium sp.		–	0.0082	–	0.0078	0.0071	0.0205
Gonyaulax spp.		–	–	–	–	–	0.0009
Prorocentrum minimum		0.0003	–	–	–	–	–
Prorocentrum micans		0.0008	–	–	–	–	–
Prorocentrum sp.		0.0073	–	–	–	–	–
Dinophysis acuta		–	–	0.0009	0.0010	0.0154	0.0037
Dinophysis norvegica		–	0.0001	0.0001	0.0001	0.0001	0.0150
Dinophysis rotundata		0.0006	0.0042	0.0030	0.0012	0.0125	0.0038
Protoceratium reticulatum		–	–	–	–	–	0.0004
Ceratium fusus		0.0001	0.0001	0.0000	0.0000	0.0003	0.0000
Ceratium spp.		0.0007	0.0001	0.0000	0.0000	0.0004	0.0018
Micracanthodinium sp.		–	–	–	–	–	0.0003
Unidentified thecate dinoflagellates		0.0002	0.0031	0.0018	0.0047	0.0038	0.0033
total	(mg m^{-2})	0.1479	1.0883	0.4160	0.4712	0.5294	0.8508

–, not found; 0.0000, <0.0004 μg C m^{-2}.

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Table 3. *Correlation coefficients between selected species of ciliates and heterotrophic dinoflagellates from a Statistical Canonical Analysis. Twenty seven taxa are tested against four environmental parameters.*

	Correlation coefficients			
STATISTIC CANONICAL ANALYSIS	Water depth	Temperature	Salinity	Chlorophyll-*a*
Protoperidinium depressum	−0.60***	−0.67***	−0.68***	0.75***
Protoperidinium bipes	0.16	−0.10	0.10	−0.66***
Protoperidinium cf. *brevipes*	0.05	−0.30	−0.16	0.07
Protoperidinium spp.	−0.40*	−0.42*	−0.38*	0.15
Diplopsalis−group	−0.37	−0.55***	−0.57***	0.07
Alexandrium sp.	−0.32	0.66***	−0.64***	0.45**
Unidentified thecate dinoflagellates	−0.30	−0.39*	−0.32	0.19
Gyrodonium cf. *spirale*	−0.30	0.03	0.20	−0.08
Gyrodinium cf. *dominans*	0.10	−0.13	−0.04	−0.14
Gyrodinuim cf. *longum*	0.01	0.29	0.26	0.23
Katodinium glaucum	−0.21	−0.59**	−0.51*	0.48*
Amphidinium sphenoides	0.21	−0.13	0.09	−0.00
Unidentified athecate dinoflagellates	−0.06	−0.51**	−0.50**	0.39
Tintinnopsis spp.	−0.18	−0.35*	−0.39*	0.11
Leprotintinnus pellucidus	−0.21	−0.36*	−0.37*	0.13
Parafavella gigantea	−0.40	−0.64***	−0.70***	0.73***
Strombidium cf. *wulfii*	−0.08	0.45**	0.24	−0.25
Strombidium cf. *pulchrum*	−0.28	−0.22	−0.18	−0.15
Strombidium spp.	−0.12	−0.05	−0.03	0.24
Laboea strobila	−0.29	−0.02	0.06	0.21
Strobilidium spp.	−0.39	−0.14	0.02	−0.15
Lohmaniella oviformis	−0.12	−0.60***	−0.53***	0.16
Myrionecta rubra	0.05	0.36*	0.18	−0.20
Scuticuciliata	−0.24	−0.43**	−0.35*	0.03

*, $P<0.05$; **, $P<0.01$; ***, $P<0.001$.

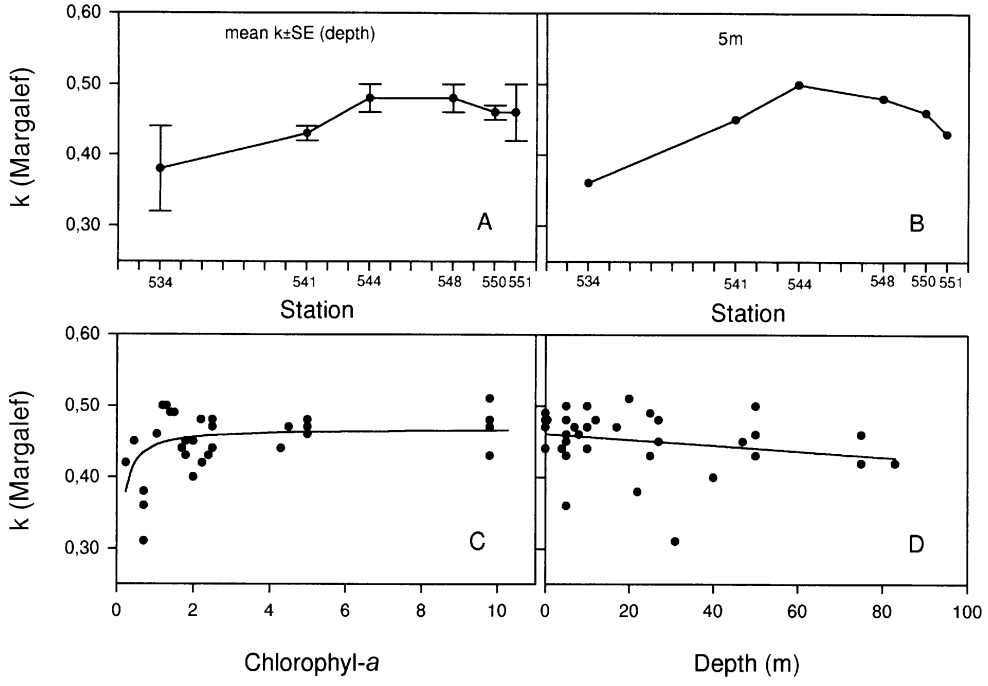

Figure 5. Margalef diversity index for (A) mean ±SE of all water depths; (B) 5 m depth; (C) k vs chlorophyll-*a* fitted by Michaelis–Menten kinetics (mean ±SE) k=(chlorophyll-*a*×0.468 ±0.010)/(chlorophyll-*a*+0.054); (D) k vs water depth k=0.461+(−4.004)×depth; (r^2=0.049).

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DISCUSSION

The present observations of overall ciliate and heterotrophic dinoflagellate biomasses were quite similar to what was reported as group-wise values by Hansen et al. (1996), who sampled along the same transect although at different sampling stations, during the same cruise. This protozooplankton biomass range (1–34 μg C l^{-1}) is not very different from observations reported from other marine waters around the world (e.g. Kiel Bight 0.05–50.0 μg C l^{-1}, Smetacek, 1981; Bering Sea and Shelikof Strait: 1.4–73.8 μg C l^{-1} Howell-Kübler et al., 1996).

Cold-water ciliates and heterotrophic dinoflagellates

Naked ciliate communities dominated by the genera *Strombidium* and *Strobilidium* have been reported before from the Barents Sea, but with no species identifications (Dale, 1986; Hansen et al., 1996). The obligate autotrophic ciliate *Mesodinium rubra* has also been reported from the Barents Sea by the same authors, and is commonly found in other cold water areas (Nielsen & Hansen, 1995; Sorokin et al., 1996; Levinsen et al., 1999). Maximum ciliate biomass reported from cold-water systems range from 5.06 μg C l^{-1} in the south-eastern Bering Sea and Shelikof Strait, Alaska (Howell-Kübler et al., 1996) to 51.59 μg C l^{-1} in the lower St Lawrence Estuary (Sime-Ngando et al., 1995). So the present biomass observations of naked ciliates are well within this range.

Tintinnid communities largely dominated by the genera *Leprotintinnus*, *Acanthostomella*, *Parafavella*, *Ptychocylis* and *Tintinnopsis* have been reported from the subarctic Bering Sea (Sorokin et al., 1996) and the eastern Canadian Arctic (Paranjape, 1987, 1988) and have been found additionally in the Barents Sea before (Dale, 1986).

Just as observed in the present study, the tintinnid biomass comprised only 5–15% of the total ciliate biomass in the Bering Sea and North Pacific (Sorokin et al., 1996), and between 0.4–1% has been reported from the Barents Sea (Dale, 1986). Tintinnids did not form more than 10% of the ciliate biomass in north-eastern Atlantic (Sleigh et al., 1996) and were a small fraction, $<2\%$, of the total ciliate numbers in the south-eastern Bering Sea and Shelikof Strait, Alaska (Howell-Kübler et al., 1996). The reported tintinnid community composition was uniform all over the Arctic waters (Dale, 1986; Paranjape, 1988; Levinsen et al., 1999), and the biomass of the tintinnid community typically is less than 10% of the total protozooplankton biomass (Dale, 1986; Sorokin et al., 1996; Sleigh et al., 1996; Howell-Kübler et al., 1996).

Athecate dinoflagellate communities dominated by *Gyrodinium*/*Gymnodium* have been reported from other waters (e.g. Nielsen et al., 1993). Small forms can be abundant during periods characterized by a low phytoplankton biomass (Hansen, 1991), but this, however, was not the case in the present investigation.

Thecate dinoflagellate communities dominated by the heterotrophic genus *Protoperidinium* have been reported from Kattegat (Hansen, 1991) and often in association with the diatom spring bloom (Hansen, 1991; Levinsen et al., 1999).

Heterotrophic dinoflagellates are an important component of the marine protozooplankton often approaching or exceeding the abundance of planktonic ciliates (Verity et al., 1993; Bralewska & Witek, 1995; Hansen et al., 1996; Levinsen et al., 1999).

Distribution factors for ciliates and heterotrophic dinoflagellates

Several key factors govern the relative distribution of ciliates and heterotrophic dinoflagellates e.g. abiotic factors such as water mass identity and ice cover, and biotic factors like food availability both in terms of biomass and particle size distribution, as well as food web interactions from grazers. Grazing upon protozooplankton by metazoans, however, is not assumed to be the major regulating factor in the present communities, since predation from larger zooplankton was reported to be insignificant (Hansen et al., 1996). Water mass identity in terms of temperature and salinity revealed no trend in relative distribution at biomass level of the protozooplankton community. However, the differences in temperature and salinity between Atlantic water and Polar water are actual regulating factors according to the Canonical Analysis at the species level, e.g. thecate dinoflagellate *Torodinium robustum* and the tintinnid *Parafavella gigantea* were associated with the true Polar water.

The overall biomass of protozooplankton followed largely the chlorophyll-*a* distribution (Figure 3B). The phytoplankton community was dominated by small-celled species to the south whereas it was dominated by large chain forming diatoms to the north (Hansen & Jensen, 2000). The Margalef diversity index showed low diversity in the open water and increasing diversity in the ice-associated water. Additionally (although not significantly) a decreasing trend in diversity with water depth. The latter likely due to decreasing food availability with depth. The diversity was correlated to chlorophyll-*a* concentration, but with a low half saturation constant. The diversity reached maximum at approximately 0.1 μg chlorophyll-*a* l^{-1}. The chlorophyll-*a* concentration increased south–north (Figure 2C). Hence, the diversity along the south–north transect was not governed by chlorophyll-*a* as the single factor. From the diversity index one cannot distinguish between species. Since some species prey upon small-celled prey (e.g. small oligotrich ciliates) and some upon larger prey (e.g. large celled heterotrophic dinoflagellates), the explanation for the observed changes in diversity could presumably be found in the composition of the phytoplankton community. In the present study a relatively high tintinnid biomass and diversity was associated with diatom blooms in the surface layer of the water column as reported by Nielsen & Richardson (1989). This diet is of limited value to strict filter feeding organisms such as naked ciliates (Jonsson, 1986) or tintinnids with limited lorica width (Heinbokel, 1978), whereas the *Protoperidinium* spp. are known to be able to feed on the chain forming diatoms by pallium-feeding (Hansen, 1991; Buskey, 1997). Also the athecate dinoflagellate *Gyrodinium* is known to engulf large chain forming diatoms (Strom & Strom, 1996). The relative importance of chlorophyll-*a* $<11\,\mu$m to chlorophyll-*a* $>11\,\mu$m was higher at the southernmost stations (Hansen & Jensen, 2000). This difference could explain why the

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naked ciliates become the dominant group of protozooplankton in the more oligotrophic water masses of the Atlantic region of the study area, since their optimal prey sizes are reported to be relatively smaller, (8:1 predator:prey ratio) (Jonsson, 1986; Fenchel & Jonsson, 1988). However, heterotrophic dinoflagellates have been shown to be important grazers of large particles often at the same size as the predator i.e. the largest phytoplankters and, in particular, diatoms (Hansen, 1991). One of the important species in the present study, *Protoperidinium pellucidum*, has been shown in laboratory experiments to grow well on, and actually actively select, diatoms (Buskey, 1997). The diversity and biomass of the thecate dinoflagellates in the present study as well as generally seems to be associated with diatom blooms in the surface layer of the water column (Nielsen et al., 1993). The biomass of ciliates and heterotrophic dinoflagellates are coupled with food resources, and the relative taxonomic composition does not follow the classical trophic cascade theory (Fenchel, 1988): the composition is governed by food concentration but in particular with prey size composition. The particle size distribution of the primary producers is an important factor regulating the functional groups due to feeding mechanisms rather than taxonomy (Hansen et al., 1994).

In conclusion, protozooplankton communities in the Barents Sea seem to be just as complex as in other marine systems including cold-water areas. This leads to a confirmation of the statement that protozooplankton species composition is generally invariant with ocean locality. It seems that analysing species composition from various localities ranging from tropical/subtropical areas through boreal and even Arctic and Antarctic studies, the qualitative species composition is relatively similar (e.g. Paranjape, 1988; Bjørnsen & Kuparinen, 1991; Sorokin et al., 1996; Levinsen et al., 1999).

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