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Horizontal distribution of microprotist community structure in the western Arctic Ocean during late summer and early fall of 2010

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Abstract The western Arctic Ocean is composed of two regions: the southern shelf and the northern basin, whereas the marine ecosystem structure is expected to vary between the regions, little information is available, particularly for the planktonic protist community. In this study, we surveyed the horizontal distribution of microprotists (diatoms, dinoflagellates and ciliates) at 59 stations in the western Arctic Ocean during September and October of 2010. The abundances of diatoms, dinoflagellates and ciliates were 0–138,640, 0–16,460 and 0–10,933 cells L^{-1}, respectively, and all of the abundances were higher on the Chukchi Sea shelf. Cluster analysis based on abundance separated the microprotist community into five groups, which contain 25, 22, 6, 4 and 2 stations. The largest group was observed on the Chukchi Sea shelf, showing a high abundance predominated by diatoms (78 % of total abundance). The second group was observed from the East Siberian Sea to the Canada Basin, characterised by low abundance and ciliate dominance (36 % of total abundance). Because of the high abundance and predominance of diatoms, the former group is characterised by eutrophic waters, which are enhanced by the continuous inflow of the nutrient-rich Pacific Water through the Bering Strait. Due to the low abundance and the dominance of ciliates, the latter group is dominated by organisms of the microbial food web. The remaining three groups were smaller and located between the two large groups. The distribution of these three groups may be based on complex physical structures, such as the anticyclonic eddy near the shelf break.

Keywords Phytoplankton · Diatoms · Dinoflagellates · Ciliates · Pacific Water · Anticyclonic eddy

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Introduction

In marine ecosystems, microprotists are composed primarily of diatoms, thecate dinoflagellates, athecate dinoflagellates and ciliates. Microprotists include both primary producers and consumers; they are preyed upon by mesozooplankton, and their horizontal distribution determines the structure of the marine ecosystem (Booth and Horner 1997; Gosselin et al. 1997; Strom and Fredrickson 2008).

In the western Arctic Ocean, diatoms are known to form a short-term pulse bloom (chlorophyll *a* (Chl *a*) exhibits peaks exceeding 8 μg L^{-1}) from late spring to summer (Springer and McRoy 1993). The high diatom abundance in the shelf of the western Arctic Ocean during summer is enhanced by the intrusion of nutrient-rich Pacific Summer Water (PSW) through the Bering Strait (Sukhanova et al. 2009; Sergeeva et al. 2010). After summer ends, Chl *a* is known to form a subsurface peak (approximately 20–40 m) under the nutrient-depleted Chukchi Sea south of the Canada Basin that may be caused by the submergence of

nutrient-rich saline PSW below the low-density (salinity <30) ice-melt water (Cota et al. 1996; Codispoti et al. 2005). Fujiwara et al. (2013) found that fucoxanthin-containing assemblages (mainly diatoms) were abundant in shallow shelf areas and that Chl *b*-containing flagellates were predominant in deep basin areas in the Chukchi Sea during summer. This evidence was based on photosynthetic pigment analysis by HPLC. These findings suggest that the taxonomic composition of the chloroplast-bearing plankton community may vary by region; however, this variability has not yet been analysed in detail.

Ciliates, including the mixotrophic ciliate *Myrionecta rubra* and heterotrophic dinoflagellates, which have frequently been observed to ingest bacteria, phytoflagellates and small diatoms (Gast 1985; Paranjape 1987; Sherr et al. 2003), are also abundant in the Arctic marine systems (Sherr et al. 1997, 2009). These heterotrophic organisms are also preyed upon by mesozooplankton (Levinsen et al. 2000; Levinsen and Nielsen 2002), giving them an important role in the microbial loop (Pomeroy 1974). In the Bering Sea and Chukchi Sea, areas adjacent to the western Arctic Ocean, high microzooplankton biomass has been reported (Taniguchi 1984; Sherr et al. 1997; Olson and Strom 2002), and evidence suggests that these microzooplankton hot spots are associated with phytoplankton blooms. However, the study areas of these studies are limited, and little information is available for not only the horizontal changes in these heterotrophic taxa but also the effects of hydrographic features in the western Arctic Ocean. Because the hydrographic features in the western Arctic Ocean vary greatly horizontally (i.e. depth varied from 50 to 3,000 m and temperature varied from −1.7 to 10 °C), these differences may affect the microprotist community; however, the details behind how these differences are important are unknown.

In the present study, we investigated the horizontal distribution of abundance and the community structure of microprotists (diatoms, thecate dinoflagellates, athecate dinoflagellates and ciliates) in the western Arctic Ocean from late summer to early fall. To evaluate horizontal changes in the community structure, microprotist assemblages were clustered based on abundance data at 59 stations covering the shelf, shelf break, slope and basin. The horizontal distribution of the microprotist community in the western Arctic Ocean is discussed from the perspective of the parameters governing their distribution.

Materials and methods

Field sampling

CTD (Sea-Bird Electronics Inc., SBE 911 Plus) casts were made at 59 stations (located at 65°46′–78°52′N, 177°43′E–151°15′W) in the western Arctic Ocean from 4 September to 13 October 2010 on R/V *Mirai*, the Japan Agency for Marine-Earth Science and Technology (JAMSTEC) (Fig. 1). Sea-ice coverage at the sampling stations was low (ca. <5 %) and composed of first-year sea ice. For enumeration and identification of protist cells, water samples (1 L) were collected from the layer of maximum Chl fluorescence (4.5–65 m), detected by a fluorescence probe (S/N 3054, Seapoint Sensors, Inc.), with a rosette of thirty-six Niskin bottles (12 L) mounted on the CTD frame. Samples were fixed and preserved with 1 % glutaraldehyde immediately after collection. Chlorophyll fluorescence values were calibrated against pure Chl *a* (Sigma Chemical Co.) before and after the cruise. For nutrient and Chl *a* measurements, seawater samples were collected from five to eight depths (Chl fluorescence maximum layer and 5, 10, 20, 30, 50, 75, 100 m, depending on bottom depth). Based on unfiltered seawater, nutrients (nitrate, nitrite, ammonium, phosphate and silicic acid) were analysed using an autoanalyser (Bran + Luebbe GmbH, TRAACS-800) on board. For each sample, 1 L sea water was filtered with a GF/F filter, the filter was immersed in N,N-dimethylformamide under dark conditions for 24 h and then Chl *a* was measured with a fluorometer (Turner Designs, Inc., 10-AU-005).

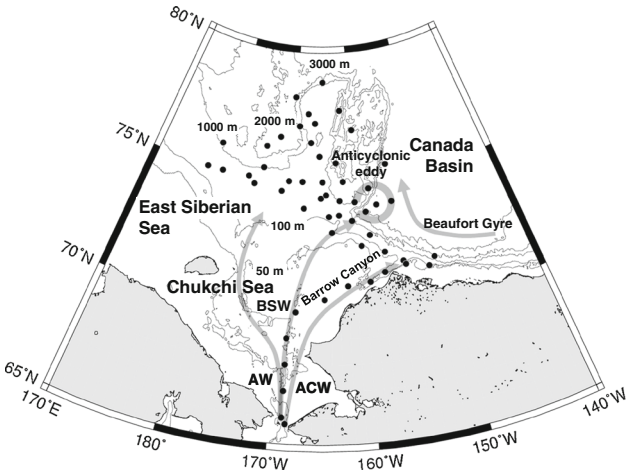

Fig. 1 Location of sampling stations in the western Arctic Ocean during 4 September 2010–13 October 2010. Arrows indicate approximate positions of current flow. The *clockwise arrow* indicates the anticyclonic eddy reported by Nishino et al. (2011). *ACW* Alaskan Coastal Water; *AW* Anadyr Water; *BSW* Bering Shelf Water

Microscopic analysis

In the land laboratory, the 1 L of preserved (1 % glutaraldehyde) water samples were stored on a stone table for more than 1 day to allow the microprotist cells to settle to the bottom of the bottle. Then, the samples were

concentrated to 20 mL using a syphon. Subsamples (0.1–0.5 mL) were mounted on a glass microscope slide, and diatoms and ciliates were counted and identified to the species level under an inverted microscope with 40–600× magnification. We counted 3–1,778 microprotist cells per sample. Because we concentrated a volume of 1 L into 20 mL, the limit of detection was 20 cells L^{-1} for a 0.1-mL subsample and 4 cells L^{-1} for a 0.5-mL subsample. Microprotists larger than 10 µm were included in this study. Minimum and maximum sizes of the cells counted during this study were 15 and 240 µm, respectively.

Species identification was made to the lowest possible level (species or genus). For species identification, we referred to Hasle and Syvertsen (1997) and Hoppenrath et al. (2009) for diatoms, and Maeda (1997) and Taniguchi (1997) for ciliates. Note that our preservative (glutaraldehyde) is an adequate fixative for diatoms and dinoflagellates but not for ciliates. Because ciliates are better preserved with acid Lugol's solution (Stoecker et al. 1994), our preservative may have biased the community composition (e.g. through loss of unloricated ciliates).

For observation of dinoflagellates, part of each subsample was stained with calcofluor (1 mg mL^{-1}) and examined under an epifluorescence microscope with UV light excitation (Fritz and Triemer 1985). Species identification of dinoflagellates followed Fukuyo et al. (1997) and Hoppenrath et al. (2009). Because the method of Fritz and Triemer (1985) was developed to count thecate dinoflagellates, there may be some underestimation in the count of athecate gymnodinoid dinoflagellates, *Gymnodinium* and *Gyrodinium* spp. It also should be noted that because the method of Fritz and Triemer (1985) does not allow for the distinction between photosynthetic and heterotrophic cells, the presence of chloroplasts within dinoflagellate cells by Chl autofluorescence was not checked. We categorised dinoflagellates as thecate and athecate species.

For other taxa (silicoflagellates, chrysophytes and radiolaria), species identification followed Throndsen (1997) and Toriumi (1997). For all taxa, cell counts were made twice, and cells were recounted if the two counts differed by more than 20 %. Using the mean value, the abundance (cells L^{-1}) of each taxon was calculated.

Data analysis

The abundances (X: cells L^{-1}) for all of the taxa were log-transformed ($Log_{10}[X + 1]$) prior to the analysis to reduce any bias in abundances. Similarities between samples were examined using the Bray–Curtis method (Bray and Curtis 1957). To group the samples, similarity indices were coupled with hierarchical agglomerative clustering with a complete linkage method (unweighted pair group method using arithmetic mean, UPGMA; Field et al. 1982). Significance tests for differences in taxon community structure between the clustered groups were performed using one-way ANOSIM tests. Non-metric multi-dimensional scaling (NMDS) ordination was conducted to delineate the sample groups on a two-dimensional map. To identify the taxa most responsible for the similarity between microprotist community groups, tests by SIMPER analysis were performed based on the abundance data. All analyses were carried out using PRIMER v6 (PRIMER-E Ltd.).

The normality of distribution and homogeneity of variance of each variable were checked before performing the regression analysis, the correlation analysis and one-way ANOVA. Multiple regression analyses ($Y = aX_1 + bX_2 + c$, where Y is the environmental variable and X_1 and X_2 are axes 1 and 2 of NMDS, respectively) were performed to clarify which environmental parameters (latitude, longitude, depth, temperature, salinity, dissolved inorganic nitrogen [DIN = nitrate + nitrite + ammonium], phosphate, silicic acid and Chl *a*) had significant relationships with the microprotist groupings. To clarify the differences between the hydrographic conditions in each group, tests by one-way ANOVA and the Tukey–Kramer HSD were performed based on the environmental variables between microprotist groups. Pearson linear correlation analyses were also performed between abundance (for total microprotists, diatoms, dinoflagellates and ciliates) and hydrographic parameters. These statistical analyses were conducted using StatView v5 (SAS Institute Inc.).

Results

Abundance

Total microprotist abundances at each station ranged between 416 and 142,624 cells L^{-1}. Diatoms ranged in density from 0 to 138,640 cells L^{-1} and composed 0–98 % of the microprotist abundance (Fig. 2a). Thecate and athecate dinoflagellates ranged in density from 0 to 14,700 and from 0 to 6,400 cells L^{-1}, respectively, and composed 0–100 % and 0–41 % of each of the total microprotist abundance (Fig. 2b, c). Ciliates ranged in density from 0 to 10,933 cells L^{-1} and composed 0–88 % of the total microprotist abundance (Fig. 2d). The horizontal distribution of diatoms had a clear regional pattern; abundance was higher in the Chukchi Sea, particularly near the Bering Strait and Barrow Canyon (Fig. 2a). Horizontal distribution patterns of thecate and athecate dinoflagellates and ciliates were similar, and both were more abundant near the Bering Strait and near an anticyclonic eddy (Nishino et al. 2011) (Fig. 2b, d).

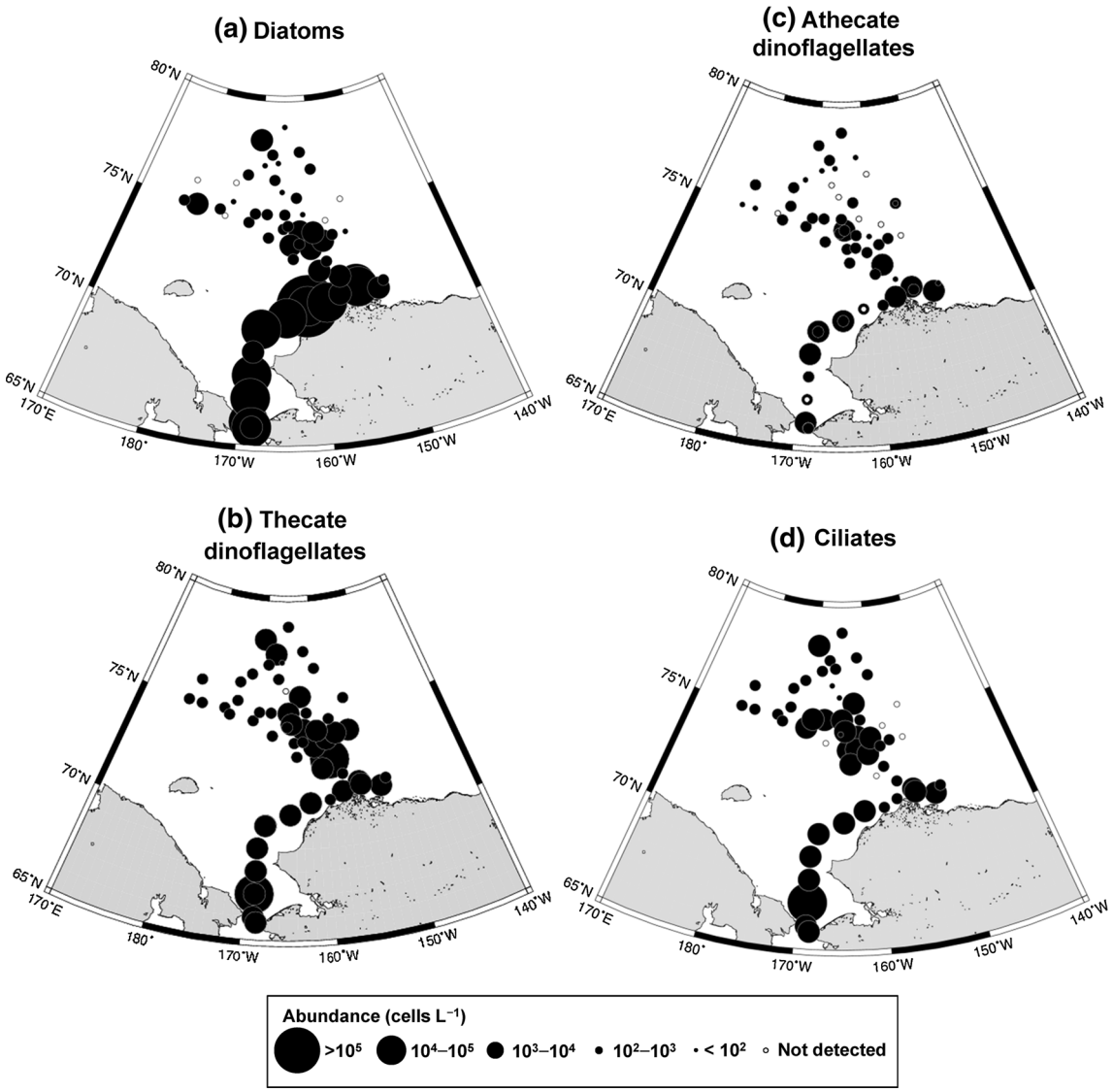

Fig. 2 Horizontal changes in the abundance of diatoms (**a**), thecate dinoflagellates (**b**), athecate dinoflagellates (**c**) and ciliates (**d**) at the depth of the maximum chlorophyll fluorescence in the western Arctic Ocean during 4 September 2010–13 October 2010

In the present study, 131 microprotist taxa were identified. These included 37 centric diatom taxa (14 different genera and 35 different species), nine pennate diatom taxa (nine different genera and five different species), 46 thecate dinoflagellate taxa (11 different genera and 39 different species), two athecate dinoflagellate taxa (two different genera and one species), nine oligotrich ciliate taxa (seven different genera and four different species), 21 tintinnid ciliate taxa (13 different genera and 14 different species), four silicoflagellate taxa (two different genera and two different species) and one taxon each of chrysophytes and radiolaria (Table 1). The dominant groups in terms of abundance were pennate diatoms (*Pseudo-nitzschia* spp. [grand mean 3,052 cells L^{-1}], *Cylindrotheca closterium* [1,169 cells L^{-1}] and *Thalassionema nitzschioides* [742 cells L^{-1}]) and centric diatoms (*Leptocylindrus minimus* [858 cells L^{-1}], *Proboscia alata* [782 cells L^{-1}] and *Chaetoceros socialis* [622 cells L^{-1}]) (Table 1). Other abundant taxa included the athecate dinoflagellate *Gymnodinium* spp. (532 cells L^{-1}), the thecate dinoflagellates *Prorocentrum minimum* (492 cells L^{-1}) and *Prorocentrum balticum* (477 cells L^{-1}) and the ciliate *Strombidium* spp. (507 cells L^{-1}).

Community structure

Cluster analysis based on abundance classified the microprotist community into five groups (A–E) at 62 and 76 % dissimilarity levels (Fig. 3a). The ANOSIM results indicated that the microprotist communities were significantly different between groups ($R = 0.752$, $p < 0.001$).

Table 1 List of protists ≥10 μm in size identified at the depth of the maximum chlorophyll fluorescence in the western Arctic Ocean during 4 September 2010–13 October 2010

Centric diatoms
- *Asteromphalus hookeri* (1)
- *Attheya longicornis* (7)
- *Attheya septentrionalis* (28)
- *Chaetoceros affinis* (9)
- *Chaetoceros atlanticus* (34)
- *Chaetoceros compressus* (93)
- *Chaetoceros concavicornis* (44)
- *Chaetoceros constrictus* (36)
- *Chaetoceros convolutus* (147)
- *Chaetoceros danicus* (12)
- *Chaetoceros debilis* (201)
- *Chaetoceros decipiens* (42)
- *Chaetoceros diadema* (188)
- *Chaetoceros didymus* (246)
- *Chaetoceros furcellatus* (201)
- *Chaetoceros simplex* (6)
- *Chaetoceros socialis* (622)
- *Chaetoceros tenuissimus* (52)
- *Chaetoceros teres* (3)
- *Chaetoceros* spp. (56)
- *Chaetoceros* spp. (resting spore) (205)
- *Coscinodiscus centralis* (2)
- *Dactyliosolen fragilissimus* (1)
- *Eucampia groenlandica* (63)
- *Leptocylindrus danicus* (174)
- *Leptocylindrus minimus* (858)
- *Melosira arctica* (33)
- *Odontella aurita* (5)
- *Planktoniella muriformis* (5)
- *Proboscia alata* (782)
- *Rhizosolenia borealis* (32)
- *Rhizosolenia setigera* (11)
- *Roperia tesselata* (3)
- *Thalassiosira constricta* (187)
- *Thalassiosira hyalina* (126)
- *Thalassiosira gravida* (26)
- *Thalassiosira nordenskioeldii* (414)

Pennate diatoms
- *Cylindrotheca closterium* (1,169)
- *Fragilaria striatula* (47)
- *Fragilariopsis* spp. (133)
- *Navicula* spp. (66)
- *Pauliella taeniata* (5)
- *Pleurosigma* spp. (17)
- *Pseudo-nitzschia* spp. (3,052)
- *Thalassionema nitzschioides* (742)
- *Thalassiothrix longissima* (50)

Thecate dinoflagellates
- *Alexandrium tamarense* (84)
- *Alexandrium* spp. (9)
- *Alexandrium* spp. (cyst) (5)
- *Dinophysis acuta* (3)
- *Dinophysis lenticula* (14)
- *Dinophysis norvegica* (37)
- *Gonyaulax polygramma* (3)
- *Gonyaulax scrippsae* (3)
- *Gonyaulax turbynei* (25)
- *Gonyaulax verior* (14)
- *Gonyaulax* spp. (40)
- *Gonyaulax* spp. (cyst) (14)
- *Heterocapsa niei* (1)
- *Heterocapsa* spp. (2)
- *Karemia brevis* (2)
- *Neoceratium arcticum* (18)
- *Neoceratium fusus* (3)
- *Neoceratium horridum* (35)
- *Neoceratium lineatum* (6)
- *Neoceratium pentagonum* (16)
- *Neoceratium tripos* (34)
- *Oxytoxum scolopax* (54)
- *Oxytoxum* sp. 1 (172)
- *Oxytoxum* sp. 2 (145)
- *Prorocentrum balticum* (477)
- *Prorocentrum compressum* (40)
- *Prorocentrum dentatum* (106)
- *Prorocentrum minimum* (492)
- *Protoperidinium avellanum* (1)
- *Protoperidinium bipes* (83)
- *Protoperidinium crassipes* (3)
- *Protoperidinium depressum* (1)
- *Protoperidinium leonis* (4)
- *Protoperidinium marukawai* (16)
- *Protoperidinium minutum* (6)
- *Protoperidinium mite* (16)
- *Protoperidinium monovelum* (3)
- *Protoperidinium pellucidum* (25)
- *Protoperidinium punctulatum* (40)
- *Protoperidinium pyriforme* (1)
- *Protoperidinium subinerme* (2)
- *Protoperidinium* spp. (14)
- *Protoperidinium* spp. (cyst) (15)
- *Pyrophacus steinii* (7)
- *Scripsiella crystallina* (5)
- *Scripsiella precaria* (1)
- Cysts (19)

Athecate dinoflagellates
- *Gymnodinium* spp. (532)
- *Gyrodinium* spp. (1)

Silicoflagelates
- *Dictyocha pseudofibula* var. *complexa* (1)
- *Dictyocha* spp. (11)
- *Distephanus speculum* var. *regularis* (3)
- *Distephanus* spp. (3)

Chrysophytes
- *Dinobryon balticum* (256)

Oligotrich ciliates
- *Laboea strobila* (2)
- *Leegaardiella* spp. (51)
- *Lohmanniella* spp. (24)
- *Parastrombidium* spp. (2)
- *Strobilidium* spp. (139)
- *Strombidium* spp. (507)
- *Tontonia appendiculariformis* (4)
- *Tontonia gracillima* (24)
- *Tontonia* spp. (4)

Tintinnid ciliates
- *Acanthostomella conicoides* (3)
- *Acanthostomella norvegica* (14)
- *Acanthostomella* spp. (3)
- *Ascampbelliella* spp. (1)
- *Cantharielle pyramidata* (5)
- *Codonellopsis frigida* (1)
- *Codonellopsis morchella* (7)
- *Codonellopsis schabi* (3)
- *Favella azorica* (163)
- *Favella* spp. (2)
- *Leprotintinnus* spp. (7)
- *Ormosella trachelium* (1)
- *Parafavella jorgenseni* (47)
- *Ptychocylis obtusa* (7)
- *Salpingacantha perca* (1)
- *Stenosemella nivalis* (13)
- *Stenosemella ventricosa* (2)
- *Stenosemella* spp. (2)
- *Tintinnidium mucicola* (150)
- *Tintinnopsis* spp. (206)

Unidentified (5)

Radiolaria (2)

Values in parentheses indicate grand mean abundance (cells L^{-1}) throughout all stations

The abundance was significantly greater in group B (mean 31,036 cells L^{-1}) than in other groups by a factor of 10 (705–3,657 cells L^{-1}) (one-way ANOVA, $p < 0.0001$). The composition of the four dominant taxa (diatoms, thecate dinoflagellates, athecate dinoflagellates and ciliates) varied among groups; the dominant taxa were ciliates in group A (36 % of total cells), diatoms in group B (78 %), ciliates in group C (59 %) and thecate dinoflagellates in group D (94 %, predominated by *Prorocentrum* spp.) (Fig. 3b). Group E had the lowest abundance (705 cells L^{-1}). Each group was also clearly separated in the NMDS plot (Fig. 3c). Various environmental parameters, including latitude, longitude, sampling depth, temperature, salinity, DIN, phosphate and Chl *a*, had significant relationships with the NMDS ordination ($r^2 = 0.12$–0.61, $p < 0.05$) (Fig. 3c).

The horizontal distributions of each sample group were well separated and varied with sea area. Group A, which occurred at the most stations (25 stations), was observed from the East Siberian Sea to the Canada Basin (Fig. 4). Group B occurred at 22 stations on the southern Chukchi Sea shelf. The other three groups (C–E), present at a few stations, were observed in the areas between groups A and B (Fig. 4).

From SIMPER analysis, 10 taxa were identified to characterise each group (Table 2). The diatoms *C. closterium* and *Th. nitzschioides* separated groups A–B, A–C, B–D, B–E and A–B, A–C, B–D, C–D, respectively. The thecate dinoflagellates *P. minimum/balticum* characterised groups A–D, B–E, D–E, respectively. The athecate dinoflagellate *Gymnodinium* spp. distinguished groups A–E, B–D, C–D, C–E. The ciliates *Strombidium* spp. and *Acanthostomella conicoides* characterised groups A–D, C–D, C–E and A–E, C–E, D–E, respectively (Table 2).

Environmental variables at each group are summarised in Table 3. Vertical profiles of environmental variables (temperature, salinity, DIN and Chl *a*) for each group are summarised in Fig. 5. The mean depth of the maximum fluorescence ranged between 19 and 50 m and was significantly deeper for groups A and D than for groups B, C and E. Mean temperature and salinity ranged from −0.71 to 2.91 °C and 29.3 to 31.3, respectively, with group B showing significantly higher temperatures and salinities. Nutrients and Chl *a* were also higher for group B in the Chukchi Sea shelf.

Discussion

Abundance

The present study revealed a large variation in the horizontal distribution of the microprotist abundance with a high abundance on the Chukchi Sea shelf and the Bering Strait in the western Arctic Sea (Fig. 2). In the Bering Strait, high primary production is supported by nutrients supplied by the continuous inflow of Pacific Water (Springer and McRoy 1993). In Barrow Canyon, a nutrient-rich upwelling current from the Canada Basin to the euphotic zone supports a high primary production (Hill and Cota 2005; Hill et al. 2005) and a high abundance of diatoms (Sukhanova et al. 2009; Sergeeva et al. 2010). In the present study, significant correlations between concentrations of nutrients and Chl *a* with diatom abundance were also observed (Table 4). Thus, the predominance of diatoms in the Bering Strait and Barrow Canyon was presumably caused by the nutrient input to these regions (Fig. 3).

The dominant taxa of the microprotist community in the present study were cosmopolitan planktonic diatoms, such as *Pseudo-nitzschia* spp., *Cylindrotheca closterium*, *Thalasionema nitzschioides*, *Chaetoceros* spp. and *Thalasiosira* spp. (Table 1). Alternatively, Sukhanova et al. (2009) also reported the dominance of centric planktonic diatoms among the phytoplankton communities during the summer in the Chukchi Sea. In addition, pennate diatoms, such as *Pauliella taeniata* and *Fragilaria oceanica*, form blooms in the early spring in the Chukchi Sea (Sukhanova et al. 2009; Sergeeva et al. 2010). Dominance of a centric diatom (*Melosira arctica*) and an ice-algae pennate diatom (*Nitzschia* spp.) near the ice edge is also reported (Booth and Horner 1997). These suggest that a large seasonal species succession exists in the microprotist assemblages in the western Arctic Ocean. In the present study period (September–October), these ice-algae and early spring diatom species were not dominant (Table 1). Cosmopolitan diatom species dominated in this study period (late summer) potentially because species successions have also been observed in the diatoms from ice algal or ice-associated species to cosmopolitan phytoplankton species (Sukhanova et al. 2009; Sergeeva et al. 2010).

Horizontal distributions of ciliates and thecate and athecate dinoflagellates were similar to those of diatoms, with the highest abundances near the Bering Strait (Fig. 2). Except for group D, thecate and athecate dinoflagellates were composed almost entirely of *Protoperidinium* and *Gymnodinium*, respectively (Table 1), including many mixotrophic and heterotrophic species (Steidinger 1997). These dinoflagellates and ciliates are reported to be high in abundance and ingest a wide variety of prey, such as diatoms, phytoflagellates and bacteria, in the Arctic Ocean during summer (Andersen 1988; Nielsen and Hansen 1995; Sherr et al. 1997). Additionally, temperature might affect the growth rates of both dinoflagellates and ciliates because strong positive correlations were confirmed between the temperature and abundances of dinoflagellates and ciliates

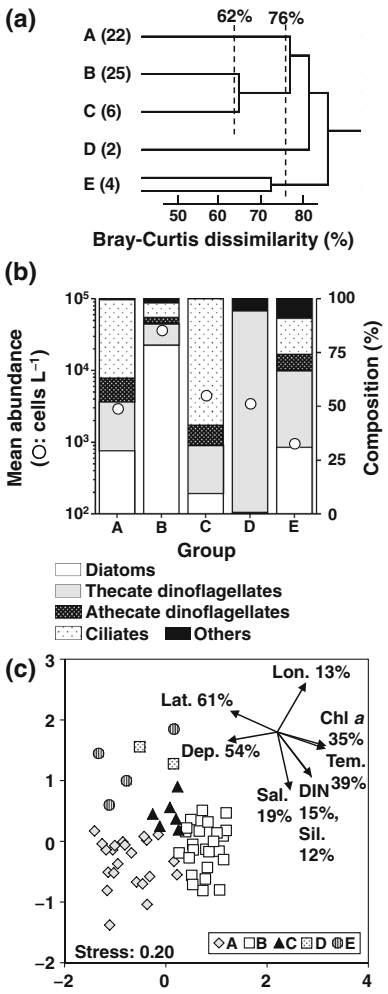

Fig. 3 Dendrogram showing the Bray–Curtis dissimilarity results based on microprotist abundance and composition (**a**). Five groups (*A–E*) were recognised at 62 and 76 % dissimilarity. *Numbers* in *parentheses* indicate the numbers of the included stations. Mean abundance and taxonomic composition of each group (**b**). Non-metric multidimensional scaling plots for each group (**c**). The directions and coefficients of determination (%) are shown for various environmental parameters. *Chl a* chlorophyll *a*, *Dep.* sampling depth, *DIN* dissolved inorganic nitrogen, *Lat.* latitude, *Lon.* longitude, *Sal.* salinity, *Sil.* silicic acid, *Tem.* temperature

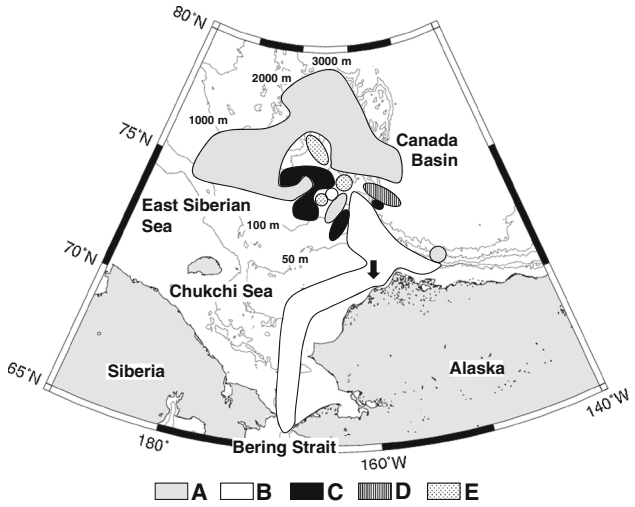

Fig. 4 Horizontal distribution of microprotist assemblages identified by Bray–Curtis dissimilarity on microprotist abundance (cf. Fig. 3a). *Solid arrow* in group B indicates the Barrow Canyon station, where the Chl *a* maximum was anomalously high and deep (cf. Fig. 5)

in the present study (Table 4). Higher temperature enhances the growth of dinoflagellates and ciliates (Hansen and Jensen 2000). Such environmental factors would affect the horizontal distribution of the microprotist community in the western Arctic Ocean during late summer (Fig. 2).

Note that our preservative (glutaraldehyde) is an adequate fixative for diatoms and dinoflagellates but not for ciliates. Because ciliates are better preserved with acid Lugol's solution (Stoecker et al. 1994), our choice of preservative may have biased the community composition (e.g. through loss of unloricated ciliates). Possibly because of shortcomings in the preservation method, ciliates were outnumbered by dinoflagellates at many stations (66 %) in this study. This may also be caused by the exclusion of small (<20 μm) dinoflagellates from the present analyses. Heterotrophic dinoflagellates are reported to have a greater abundance than ciliates in the Arctic Ocean during the summer (Andersen 1988; Nielsen and Hansen 1995; Sherr et al. 1997). In the Arctic Ocean, temperature may be a primary factor controlling the growth rates of both dinoflagellates and ciliates (Hansen and Jensen 2000). Strong positive correlations were confirmed between temperature and abundances of dinoflagellates and ciliates in the present study (Table 4), which is consistent with the results of previous studies.

In addition to these bottom-up regulations in the abundances of microprotists, top-down control, mainly by copepod grazing, is also known to be important (Levinsen and Nielsen 2002). Both net zooplankton abundance and biomass during the same cruise showed regional differences between the shelf and basin: abundance was 3.4 times greater and biomass was 2.9 times greater, in the shelf than in the basin (Matsuno unpublished data). From these parallel interactions between microprotist abundance and net-mesozooplankton abundance and biomass (both higher in the Chukchi Sea shelf), bottom-up control from primary producers may dominate throughout the microprotist and mesozooplankton communities in this region.

Community structure

Five community groups were identified based on the microprotist abundance data. The horizontal distributions of each community group were distinct: the large community groups A and B occurred at the basin and shelf,

Table 2 Ranking of taxa according to their relative contribution (%) to the multivariate similarities between pairs of the microprotist groups (A–E), defined by the cluster analysis in the western Arctic Ocean during 4 September–13 October 2010 (cf. Fig. 3a)

Group	A	B	C	D
B	*Cylindrotheca closterium* (4 %)			
	Pseudo-nitzchia spp. (3 %)			
	Thalassionema nitzschioides (3 %)			
C	*Thalassionema nitzschioides* (5 %)	*Pseudo-nitzchia* spp. (3 %)		
	Cylindrotheca closterium (4 %)	*Chaetoceros* spp. (resting spore) (3 %)		
	Oxytoxum sp. 1 (4 %)	*Proboscia alata* (3 %)		
D	*Prorocentrum minimum* (9 %)	*Cylindrotheca closterium* (5 %)	*Strombidium* spp. (8 %)	
	Prorocentrum balticum (8 %)	*Gymnodinium* spp. (4 %)	*Gymnodinium* spp. (8 %)	
	Strombidium spp. (8 %)	*Thalassionema nitzschioides* (4 %)	*Thalassionema nitzschioides* (7 %)	
E	*Acanthostomella conicoides* (6 %)	*Cylindrotheca closterium* (4 %)	*Gymnodinium* spp. (6 %)	*Prorocentrum minimum* (14 %)
	Gymnodinium spp. (6 %)	*Prorocentrum minimum* (4 %)	*Strombidium* spp. (5 %)	*Prorocentrum balticum* (11 %)
	Oxytoxum sp. 2 (6 %)	*Pseudo-nitzchia* spp. (3 %)	*Acanthostomella conicoides* (5 %)	*Acanthostomella conicoides* (9 %)

Table 3 Comparisons of environmental variables (water temperature, salinity, nitrate, nitrite, ammonium, DIN, phosphate, N:P ratio and silicic acid) and chlorophyll a concentrations at the depth of the chlorophyll fluorescence maximum for the five groups (A−E) in the western Arctic Ocean during 4 September−13 October 2010. The five groups were identified from Bray-Curtis dissimilarity based on protist abundance (cf. Fig. 3a). Results are shown as mean ± standard deviation. Differences between groups were tested by one-way ANOVA with the Tukey-Kramer HSD post-hoc test. Any groups not connected by underlines are significantly different ($p < 0.05$)

Environmental variables	Groups					one-way ANOVA	Tukey-Kramer HSD
	A (22)	B (25)	C (6)	D (2)	E (4)		
Fluorescence maximum depth (m)	48 ± 11	20 ± 9	19 ± 9	50 ± 21	30 ± 4	***	C B E A D
Temperature (°C)	−0.57 ± 1.16	2.91 ± 2.77	1.54 ± 0.42	−0.71 ± 0.08	0.10 ± 0.62	***	D A E C B
Salinity	31.1 ± 0.5	31.3 ± 1.2	29.3 ± 1.2	30.5 ± 0.4	29.9 ± 1.5	**	C E D A B
Nitrate (μM)	1.78 ± 2.23	2.87 ± 4.18	0.04 ± 0.03	0.07 ± 0.07	0.25 ± 0.42	NS	
Nitrite (μM)	0.12 ± 0.09	0.07 ± 0.07	0.01 ± 0.01	0.06 ± 0.06	0.02 ± 0.04	**	C E D B A
Ammonium (μM)	0.09 ± 0.15	1.04 ± 1.25	0.11 ± 0.04	0.02 ± 0.01	0.17 ± 0.23	**	D A C E B
DIN (μM)	2.02 ± 2.42	4.03 ± 5.26	0.16 ± 0.06	0.17 ± 0.12	0.45 ± 0.71	NS	
Silicic acid (μM)	6.72 ± 4.07	9.42 ± 9.72	2.70 ± 0.32	3.84 ± 0.58	3.82 ± 1.16	NS	
Phosphate (μM)	0.92 ± 0.20	0.88 ± 0.45	0.62 ± 0.03	0.78 ± 0.04	0.75 ± 0.09	NS	
N:P ratio (μM:μM)	1.88 ± 1.66	3.21 ± 3.24	0.25 ± 0.09	0.21 ± 0.15	0.54 ± 0.83	*	Not detected
Chlorophyll *a* (μg L^{-1})	0.38 ± 0.22	1.14 ± 0.85	0.42 ± 0.06	0.22 ± 0.04	0.30 ± 0.13	**	D E A C B

Numbers in parentheses indicate the number of stations included in each group.

NS not significant

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

respectively, and the three small community groups (C–E) occurred between the two large community groups (Fig. 4).

Group A was widely distributed from the East Siberian Sea to the Canada Basin (Fig. 4). The hydrography where group A occurred was characterised by low temperature, low nutrients and a low Chl *a* peak in the subsurface layer (mean 48 m) (Fig. 5). The relatively high composition of ciliates (36 %) (Fig. 3b) suggests the dominance of

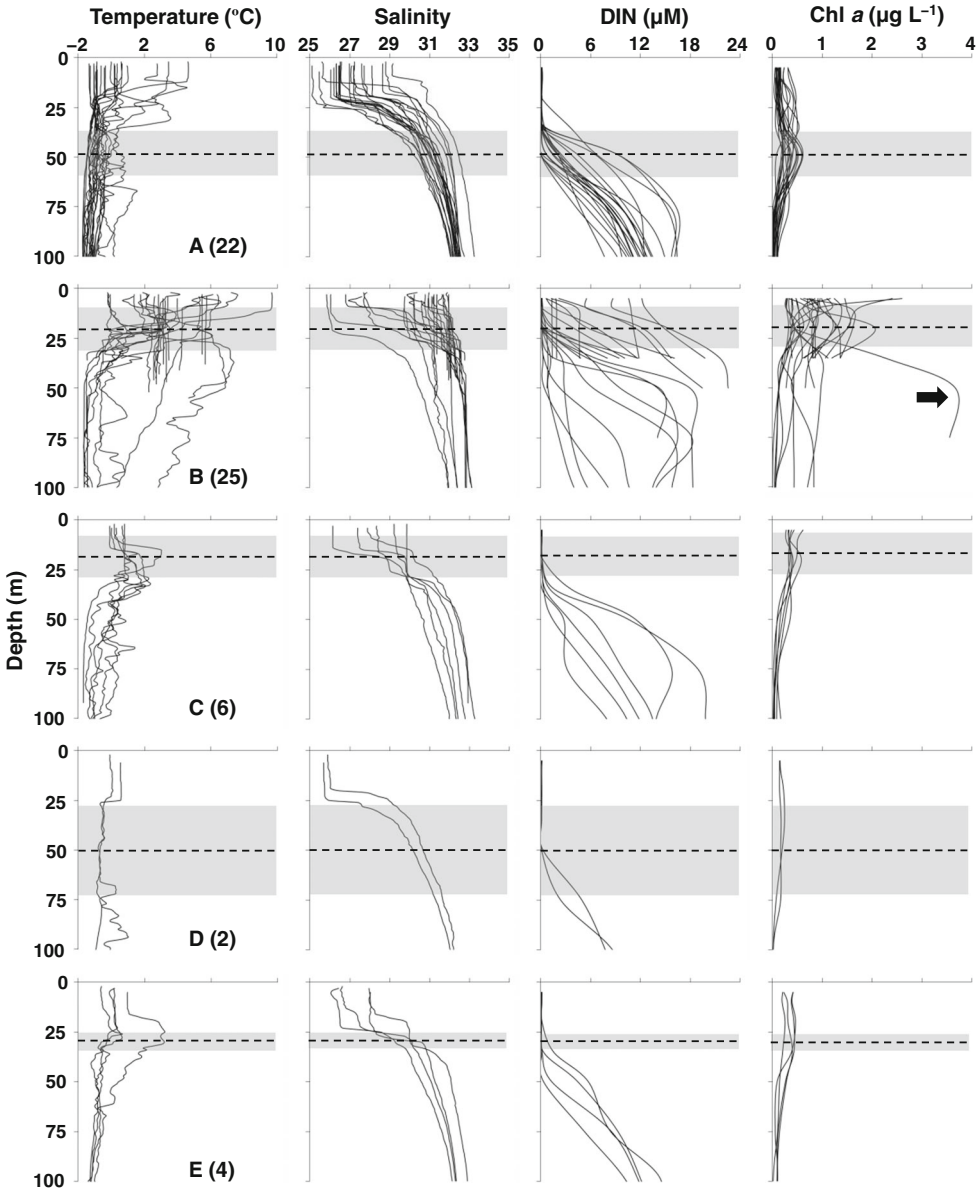

Fig. 5 Vertical profiles of hydrographic parameters for each sample group. *Horizontal dashed lines* and *shadings* indicate means and standard deviations of sampling depths, respectively. The *arrow* in the Chl *a* panel for group B indicates the maximum in the deep layer (50 m) at the Barrow Canyon station (cf. Fig. 4)

Table 4 Matrix of correlation coefficients (*r*) between the abundances of four protist groups and environmental variables

Environmental variables	Diatoms	Thecate dinoflagellates	Athecate dinoflagellates	Ciliates	Total protists
Sampling depth (m)	NS	−0.515***	−0.346**	−0.486***	−0.335**
Temperature (°C)	NS	0.657***	0.357**	0.413***	0.321*
Salinity	0.374**	NS	NS	NS	0.366**
DIN (μM)	0.422***	NS	NS	NS	0.400**
Silicic acid (μM)	0.410***	NS	NS	NS	0.379**
Phosphate (μM)	0.304*	−0.285*	NS	NS	NS
N:*P* ratio (μM:μM)	0.335**	NS	0.270*	NS	0.333*
Chlorophyll *a* (μg L^{-1})	0.573***	0.308*	0.420**	NS	0.567***

Note that "total protists" includes all the protist taxa listed in Table 1

NS not significant

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

microbial loop organisms (Pomeroy 1974). Cota et al. (1996) found relatively high microbial community respiratory rates in the eastern Chukchi Sea during summer, where nitrate was vertically depleted in the upper mixed layer. Bacterivorous ciliates abundantly occurred after phytoplankton bloom during late summer in Disko Bay, western

Greenland (Levinsen et al. 2000). Thus, the basin of the western Arctic Ocean during late summer was oligotrophic, and the microprotists were dominated by organisms involved in the microbial loop (Sherr et al. 1997, 2003).

Group B was observed on the Chukchi Sea shelf, and it had the highest abundance, predominated by diatoms. This area was characterised by higher temperature, salinity, nutrients and Chl *a*, which peaked in the surface layer (mean 20 m) (Fig. 5). All of these physical characteristics were caused by the warm, saline and nutrient-rich Pacific Water that flowed through the Bering Strait (Springer and McRoy 1993). The characteristic species of group B was the diatom *Th. nitzschioides* (Table 2). *Th. nitzschioides* is a cosmopolitan species common in cold water, particularly in the polar regions (Degerlund and Eilertsen 2010). An anomalously high Chl *a* concentration was detected at 50 m depth in the Barrow Canyon (Fig. 5). In the Barrow Canyon, because of ice melt, low-salinity water is present at the surface, and high-salinity Pacific Water usually sinks below the low-salinity water (Codispoti et al. 2005). Diatoms transported with the submerged Pacific Water below ice-melt water presumably utilise the relatively high nutrients in the deep layer and form the subsurface Chl *a* peak (Hill and Cota 2005; Hill et al. 2005; Sergeeva et al. 2010).

Group C was predominated by ciliates, and the representative species was *Strombidium* spp. (Fig. 3b; Table 2). The oligotrich *Strombidium* spp. are small (20–30 μm in this study) and graze on bacteria and small phytoplankton (Capriulo and Carpenter 1983; Gast 1985; Paranjape 1987). Temperature is generally a major factor controlling the growth rate of ciliates, and ciliates tend to grow faster than dinoflagellates, especially at low temperatures (Hansen and Jensen 2000). Group C occurred near group B, which was characterised by high abundance. Group C occurred in more oligotrophic and lower temperature water than group B (Fig. 5). These findings suggest that the abundant small pennate diatoms (<10 μm) and nanophytoplankton (e.g. prymnesiophytes and haptophytes, Coupel et al. 2012) on the Chukchi Sea shelf (group B) were transported to the shelf break and were grazed actively by oligotrich ciliates (group C).

According to Nishino et al. (2011), an anticyclonic eddy (100 km in diameter) was formed on the Chukchi Sea slope due to an increase in the volume of Alaskan Coastal Water (ACW) along the Barrow Canyon. Group D occurred north of the anticyclonic eddy (Figs. 1, 4) and was dominated by thecate dinoflagellates (Fig. 3b); the representative species were the autotrophic *P. minimum* and *P. balticum* (Table 2). Because this anticyclonic eddy temporally retains Pacific Water from the shelf to the basin, the area where group D occurred was less affected by Pacific Water, i.e. low salinity and low nutrients. Because dinoflagellates can swim, they can grow faster in lower nutrient concentrations than can diatoms by performing diel vertical migration (Margalef 1979). Because of the strong stratification in the Chukchi Sea during summer, autotrophic and heterotrophic dinoflagellates dominate in the surface layer (Sergeeva et al. 2010). The oligotrophic conditions may have caused the predominance of dinoflagellates in group D.

Group E had the lowest abundance (Fig. 3b), and it was hydrographically connected with group C (Fig. 5). Groups C and E occurred near each other and in similar hydrographic conditions, but they showed differences in microprotist abundance and species composition. As mentioned above, group C was abundant and predominated by the oligotrich ciliates *Strombidium* spp., whereas group E was characterised by fewer ciliates (Table 2; Fig. 3b). Because group E occurred north of group C (Fig. 4), group E was farther from the nutrient input of the Pacific Water. In the Arctic Basin during summer, copepods have been reported to consume 36 % of the primary production and prefer micro-sized (20–200 μm) mobile heterotrophic protists as food rather than photosynthetic protists (Campbell et al. 2009). For the lowest abundance of group E, because of the copepod predation, the abundance of mobile heterotrophic ciliates would be lower than in group C.

In conclusion, the horizontal distribution of microprotists in the western Arctic Ocean during late summer exhibited substantial regional variation. On the shelf, the predominance of diatoms was attributed to the continuous inflow of nutrient-rich Pacific Water. In the basin, the effects of the Pacific Water were diminished, and the microbial loop became dominant. On the continental slope between those two regions, the microprotist communities tended to exhibit greater spatial differences. This finding is presumably related to the complex physical oceanographic structures in this region, including anticyclonic eddies.

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