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1

2 **Neritic tintinnid community structure and mixing with oceanic tintinnids in shelf**
3 **waters of the Pacific Arctic Region during summer**

4

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20

21 **Abstract:**

22 Tintinnids play an important role in the microbial food web and consist of neritic and oceanic ones
23 biogeographically. Neritic tintinnid species are mainly present in continental shelf areas. Knowing their
24 community structure is thus critical to better understand the ecological function of microzooplankton in
25 the Pacific Arctic Region. During the summer of 2019, neritic tintinnid diversity, vertical distribution,
26 and mixing with oceanic tintinnids were investigated from the Bering Sea to the Chukchi Sea. A total
27 of 19 neritic tintinnid species belonging to 5 genera were identified. All of the neritic species were
28 reported in waters south of the Pacific Arctic Region. No endemic Arctic neritic tintinnid was found.
29 The distributions of nine abundant neritic species exhibited no difference between the Bering Sea and

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30 Chukchi Sea. Abundant neritic species were divided into surface- and bottom-dwellers according to
31 their vertical distributions. Bering Shelf Water was dominated by neritic bottom-dwellers, while
32 Anadyr Water was inhabited by neritic surface-dwellers. Neritic and oceanic tintinnids from the Pacific
33 were mainly advected into the Chukchi Sea by Bering Shelf Water. Neritic bottom-dwellers could be
34 mixed into surface waters possibly due to upwelling caused by Pacific Inflow Water flow over shelves.
35 In surface waters, the neritic tintinnid community represented < 50% of the total tintinnid abundance.
36 Our results will help to predict future changes in the microzooplankton community under the influence
37 of global warming and increasing Pacific Inflow Water on the Pacific Arctic Region shelf as well as in
38 the Arctic basin.

39 **Key words:** Neritic tintinnid; Community structure; Vertical distribution; Mixing; Pacific Arctic
40 Region

41

42 **1. Introduction**

43 Tintinnids (Ciliophora - Spirotrichea - Choreotrichia) are planktonic ciliates with loricae around
44 their body (Lynn, 2008), and are observed in marine habitats worldwide. Lorica shape is an important
45 taxonomic feature that enables species identification. Tintinnids are regarded as model organisms for
46 marine plankton research (Dolan et al., 2013; Wang et al., 2021). They are primary consumers of pico-
47 (0.2 - 2 μm) and nano- (2 - 20 μm) sized producers, as well as important food sources of metazoans and
48 fish larvae (Stoecker et al., 1987; Dolan et al., 1999; Gómez, 2007). Therefore, tintinnids play an
49 important role in the flow of matter and energy from the microbial food web into the traditional food
50 chain (Azam et al., 1983; Pierce and Turner, 1992; Calbet and Saiz, 2005). Biogeographically,
51 tintinnids are distinguished as neritic and oceanic genera (Pierce and Turner, 1993; Dolan et al., 2013).

52 Neritic tintinnid species are restricted to nearshore shelf waters (Dolan et al., 2013).

53 The Pacific Arctic Region, including the Bering Sea and the Chukchi Sea, is an inflow shelf of the
54 Arctic Ocean as well as one of the largest shelf seas in the world (Grebmeier and Maslowski, 2014;
55 Wassmann et al., 2015). However, neritic tintinnids in the Pacific Arctic Region are poorly documented
56 except for a list of neritic tintinnid species in the Chukchi Sea compiled by Dolan et al. (2017)
57 according to previous reports. In the Bering Sea shelf waters, Taniguchi (1984), Li et al. (2016a) and
58 Kršinić (2018) reported lists of neritic tintinnid species.

59 Pacific Inflow Water (PIW) flowing from the Pacific into the Arctic Ocean has a strong influence
60 on the plankton community in the Pacific Arctic Region. From the Bering Sea to the Arctic Ocean,
61 phytoplankton and other protists are divided into cosmopolitan, boreal/warm-temperate, Arctic-boreal
62 and Arctic species (Lin et al., 2013; Wang et al., 2018), and three mesozooplankton communities are
63 distinguished: southern Chukchi Sea, central and northern Chukchi Sea and deep-sea communities (Xu
64 et al., 2016, 2018). From the Bering Sea to the Arctic Ocean, the oceanic tintinnid community (boreal)
65 is further divided into subarctic- and Arctic assemblages (Wang et al., 2019). Whether neritic tintinnids
66 could be divided into subarctic- and Arctic assemblages is unknown.

67 From west to east in the Bering Strait, three water masses (Anadyr Water, Bering Shelf Water and
68 Alaskan Coastal Water) of PIW flow parallelly with obvious hydrographic characteristics (Springer et
69 al., 1996; Longhurst 1998; Steele et al., 2004; Zhao et al., 2006; Pisareva et al., 2015; Hunt et al., 2016).
70 Anadyr Water (-0.3 - 2.5°C, 32.5 - 33.1) had lower temperature but higher salinity than Alaskan
71 Coastal Water (2.5 - 10.5°C, 28.6 - 31.8) (Coachman et al., 1975; Liu et al., 2016). Species
72 compositions of both phytoplankton (Coupel et al., 2011; Lin et al., 2018; Wang et al., 2018) and
73 mesozooplankton (Springer et al., 1989; Hopcroft et al., 2005; 2010) are different in Anadyr Water and

74 Alaskan Coastal Water. Therefore, we speculate that tintinnid species composition and abundance
75 might also be different in each water mass of PIW.

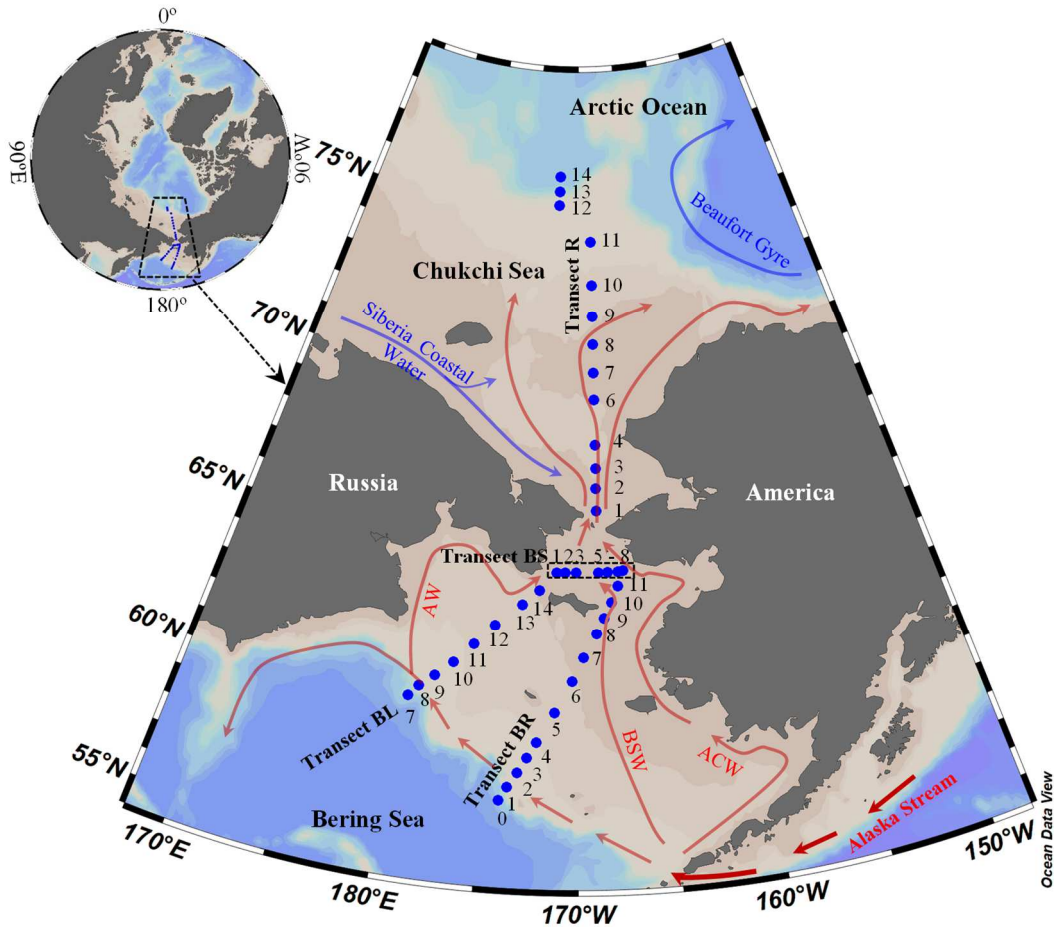
76 In most of the shelf areas, the oceanic and neritic plankton communities are separated by the
77 coastal front (Li et al., 2016b). Neritic tintinnids tend to live in waters near the seafloor in the East
78 China Sea (Yu et al., 2016). However, in the Pacific Arctic Region, three water masses of the PIW flow
79 into the Arctic Ocean through the surface layer and respond rapidly to the local wind with high spatial
80 coherence over the basin scale (Woodgate et al., 2005; Pisareva et al., 2015), which thus inevitably
81 caused fronts and vertical mixing with bottom waters of the Pacific Arctic Region. This mixing may
82 produce upwelling or downwelling in the front area and non-stratification water downstream (Piatt and
83 Springer, 2003; Zhao et al., 2006), and eventually result in a mixed assemblage of neritic and oceanic
84 assemblage of tintinnids. A high abundance of oceanic tintinnids appear in the surface waters,
85 consistent with the position of PIW (Wang et al., 2019). However, the influence of oceanic tintinnids on
86 neritic community has not been studied until now.

87 In this study, we investigated the neritic tintinnid community structure and mixing with oceanic
88 tintinnids in shelf waters of the Pacific Arctic Region during summer, when PIW is at its annual
89 maximum flux (Wassmann et al., 2015). We aimed to determine (i) whether there are endemic Arctic
90 neritic species in the Chukchi Sea shelf water; (ii) the difference in tintinnid assemblages between the
91 eastern and western sides of the Bering Strait; and (iii) the role of vertical mixing on the distribution of
92 neretic and oceanic tintinnids. The output of this study is expected to be of great help in monitoring and
93 forecasting the planktonic ecosystem response to global warming.

94

95 **2. Materials and methods**

96 Sampling was conducted from August 27 to September 8, 2019 during the 10th Chinese National
97 Arctic Research Expedition aboard R.V. “Xiangyanghong 01” (Table 1). Water samples were collected
98 at 40 stations along four transects covering the Bering Sea shelf (Transect BL, Sts. BL7 - BL14,
99 Transect BR, Sts. BR0 - BR11), Bering Strait (Transect BS, Sts. BS1 - BS3 and BS5 - BS8), and
100 Chukchi Sea shelf (Transect R, Sts. R1 - R4 and R6 - R14) (Fig. 1; Table 1). Water depths at most
101 stations were shallower than 200 m. At each station, vertical profiles of temperature and practical
102 salinity were obtained from the surface to seafloor (or 200 m with depth deeper than 200 m) using a
103 conductivity-temperature-pressure probe (Sea-Bird Electronics, Bellevue, WA, USA). At each station,
104 water samples were taken at three to seven sampling depths in the upper 200 m of the water column
105 using 12 L Niskin bottles attached to a rosette wheel of the CTD. All the stations were free of sea ice.



106

107 **Fig. 1.** Transects and survey stations from the Bering Sea to the Arctic Ocean. Red arrows: Pacific
 108 inflow waters (Springer et al. 1996; Longhurst 1998; Steele et al. 2004; Hunt et al., 2016); AW: Anadyr
 109 Water; BSW: Bering Shelf Water; ACW: Alaskan Coastal Water.

110

111 **Table 1**

112 List of stations with date sampled and environmental factor range (temperature (T, °C), salinity
 113 and Chlorophyll *a* concentration (Chl *a*, µg L⁻¹) range from surface to bottom or 200 m)

Station	Date	Latitude	Longitude	Depth (m)	T	Salinity	Chl <i>a</i>
BL7	8/27/2019	60.0359°N	179.5127°W	1521	3.4-11.1	32.8-33.3	0.02-3.98
BL8	8/27/2019	60.3992°N	179.0013°W	1435	3.1-10.7	32.9-33.2	0.01-0.77
BL9	8/27/2019	60.7973°N	178.2111°W	157	2.3-11.2	32.9-33.0	0.02-2.89
BL10	8/28/2019	61.2857°N	177.2399°W	118	2.4-10.8	32.5-32.9	0.03-0.56
BL11	8/28/2019	61.9258°N	176.1754°W	113	1.5-10.2	32.3-32.6	0.06-0.91
BL12	8/28/2019	62.5934°N	175.0103°W	76	0.0-10.4	32.1-32.3	0.09-0.99
BL13	8/28/2019	63.29°N	173.4367°W	66	0.2-10.6	32.2-32.6	0.20-0.90
BL14	8/28/2019	63.7666°N	172.4077°W	44	1.0-10.2	32.2-32.9	0.09-1.38
BS1	8/29/2019	64.3224°N	171.3899°W	42	3.1-3.4	33.0-33.1	0.53-0.59
BS2	8/29/2019	64.3342°N	170.8207°W	41	2.1-2.6	32.8-32.9	0.32-0.43
BS3	8/29/2019	64.3278°N	170.1292°W	43	3.2-3.5	33.0-33.0	0.69-0.97
BS5	8/29/2019	64.3302°N	168.7089°W	40	3.9-9.4	31.6-32.6	0.96-2.88
BS6	8/29/2019	64.3289°N	168.1097°W	35	6.8-9.8	32.0-32.3	1.29-1.71

BS7	8/29/2019	64.3344°N	167.4518°W	30	3.0-8.8	31.3-32.1	1.06-1.11
BS8	8/29/2019	64.3653°N	167.1212°W	31	5.1-10.8	30.7-32.0	0.71-0.83
R1	8/30/2019	66.2106°N	168.7527°W	55	2.4-7.6	31.7-32.8	2.87-17.75
R2	8/30/2019	66.8942°N	168.7482°W	43	2.6-6.3	32.4-32.7	1.80-7.61
R3	8/30/2019	67.4948°N	168.7498°W	51	2.7-8.8	31.9-32.7	1.27-8.53
R4	8/30/2019	68.1927°N	168.7606°W	60	3.1-6.8	32.6-32.9	0.43-2.01
R6	8/30/2019	69.5333°N	168.7512°W	51	5.8-9.7	30.5-32.5	0.23-1.55
R7	8/31/2019	70.3332°N	168.7503°W	41	0.8-8.9	31.7-32.6	0.50-0.80
R8	8/31/2019	71.1732°N	168.7545°W	49	2.5-8.5	30.8-32.6	0.16-0.57
R9	8/31/2019	71.9933°N	168.7373°W	50	1.9-8.0	30.8-32.8	0.75-2.04
R10	8/31/2019	72.8982°N	168.7448°W	61	-1.5-5.1	29.3-32.6	0.18-0.94
R11	8/31/2019	74.1556°N	168.7541°W	172	-1.5-4.8	29.0-34.4	0.02-0.47
R12	9/02/2019	75.207°N	172.0089°W	480	-1.6-0.9	28.0-34.6	0.01-0.22
R13	9/02/2019	75.6067°N	171.996°W	1498	-1.6-0.5	28.2-34.5	0.01-0.28
R14	9/02/2019	76.0337°N	171.9799°W	2012	-1.6-0.1	28.1-34.4	0.01-0.21
BR11	9/06/2019	63.9011°N	167.4781°W	35	5.9-7.4	31.9-31.9	1.72-2.91
BR10	9/06/2019	63.4013°N	167.9389°W	30	4.2-5.6	31.9-32.0	1.91-4.71
BR9	9/06/2019	62.9067°N	168.4268°W	40	3.2-10.0	31.9-32.1	0.79-1.74
BR8	9/07/2019	62.4053°N	168.8968°W	37	3.4-10.9	31.2-31.5	0.32-1.11
BR7	9/07/2019	61.653°N	169.6772°W	39	6.5-10.8	31.5-31.7	0.53-1.79
BR6	9/07/2019	60.9051°N	170.3536°W	51	4.7-11.1	31.9-32.0	0.25-1.19
BR5	9/07/2019	59.8991°N	171.3069°W	71	3.0-11.2	32.0-32.3	0.17-1.05
BR4	9/08/2019	58.9074°N	172.2544°W	96	3.8-11.4	32.3-32.7	0.06-1.41
BR3	9/08/2019	58.4049°N	172.7352°W	115	4.0-11.1	32.5-32.8	0.01-1.47
BR2	9/08/2019	57.9018°N	173.2263°W	118	4.3-11.1	32.5-32.9	0.06-0.52
BR1	9/08/2019	57.405°N	173.6983°W	124	4.5-10.8	32.4-33.0	0.02-1.20
BR0	9/08/2019	56.9533°N	174.0913°W	1673	3.6-11.3	32.6-33.4	0.01-3.73

114

115 The Chlorophyll *a* (Chl *a*) concentration was determined by filtering 250 mL of seawater through
116 a Whatman GF/F glass fiber filter. Plankton retained on the filter were extracted in 90% (vv⁻¹) acetone.
117 Fluorescence was measured according to the Joint Global Ocean Flux Study (JGOFS) protocol (Knap
118 et al., 1996) using a Turner Trilogly fluorometer Model 10.

119 For tintinnid analysis, water samples (1 L) from each sampled depth were fixed with acidic
120 Lugol's solution (1% final concentration) and stored in darkness at 4°C. In the laboratory, water
121 samples were concentrated to volumes of approximately 200 mL by siphoning off the supernatant after
122 settling the sample for 60 h. This settling and siphoning process was repeated until a final concentrated

123 volume of 50 mL was achieved, which was then settled in two Utermöhl counting chambers (25 mL per
124 chamber) (Utermöhl, 1958) for at least 24 h. All samples were examined using an Olympus IX 73
125 inverted microscope (100× or 400×). Because mechanical and chemical disturbance during collection
126 and fixation could provoke detachment of the protoplasm from the loricae (Paranjape and Gold, 1982;
127 Alder, 1999), cell counts included empty tintinnid loricae. Our abundance result might be an
128 overestimate because some loricae might have been empty at the time of sampling (Kato and Taniguchi,
129 1993; Dolan et al., 2017).

130 According to morphology and size, tintinnid species were identified to species following Kofoid
131 and Campbell (1929, 1939), Hada (1937), Taniguchi (1976), Davis (1977, 1981), Zhang et al. (2012),
132 Dolan et al. (2014, 2017) and Kršinić (2018). Where possible, the sizes of at least 10 loricae of each
133 species were measured. Tintinnid species in genera *Helicostomella*, *Leprotintinnus*, *Metacylis*,
134 *Stenosemella* and *Tintinnopsis* were identified as neritic following Dolan et al. (2013). The vertical
135 distribution of oceanic tintinnids from the Bering Sea to the Arctic Ocean in 2016 was studied in Wang
136 et al. (2019). We just exhibited oceanic tintinnid species-specific data in Transect BS in this study. The
137 classification of three water masses belonged to PIW in Transect BS was based on salinity (Coachman
138 et al., 1975; Liu et al., 2016). SPSS version 16 statistical software was used to perform correlation
139 analysis.

140

141 **3. Results**

142 **3.1. Hydrographic features**

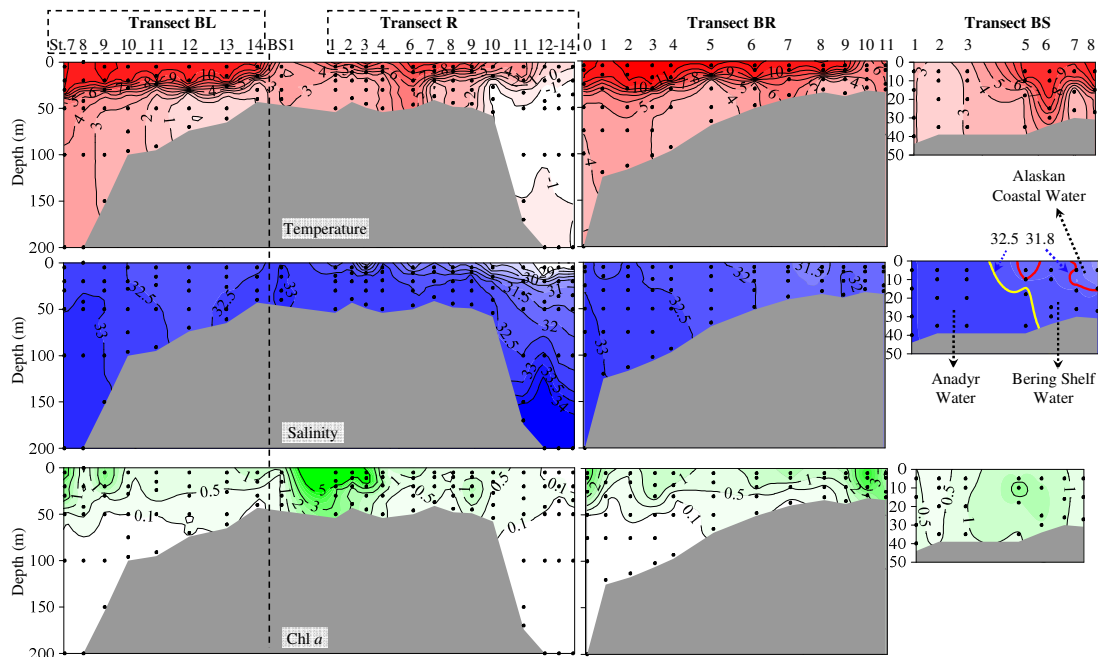
143 Horizontally, surface temperature (range of 0.1 - 11.4°C) and salinity (range of 28.0 - 33.0)
144 decreased from the Bering Sea (Transects BL and BR) to the Chukchi Sea (Transect R) (Fig. 2).

145 Vertically, temperature decreased from the surface to bottom (or 200 m depth in stations with bottom
146 depths deeper than 200 m) in both the Bering Sea and the Bering Strait. There was a thermocline at
147 approximately 40 m depth. The 5°C isotherm occurred at depths of approximately 50 m in Transects
148 BL and BR, and was shallower (approximately 20 m) in Transect R. In the northern Chukchi Sea (Sts.
149 R10 - R14), low temperature water (< -1°C) appeared at depths from 30 to 150 m (Fig. 2).

150 Surface salinity was higher at the southern stations of the Bering Sea (Transects BL and BR) than
151 at the northern stations of the Chukchi Sea (Transect R). Salinity was vertically uniform in the Bering
152 Sea and stratified in the northern part of the Chukchi Sea (salinity increased from surface to bottom or
153 200 m depth) (Fig. 2). Surface Chlorophyll *a* (Chl *a*) concentrations were highest (17.75 µg L⁻¹) in the
154 middle of the Bering Strait (St. R1) (Fig. 2). Higher Chl *a* concentrations occurred in the upper 50 m
155 throughout the water column.

156 In Transect BS, the water column was vertically mixed with the vertical 5°C isotherm and 32.5
157 isohaline separating Anadyr Water (AW) and Bering Shelf Water (BSW). The upper 10 m water in Sts.
158 BS5, BS7 and BS8 belonged to Alaskan Coastal Water (ACW) according to the 31.8 isohaline. Water
159 column salinity ranging between 31.8 and 32.5 belonged to BSW (Fig. 2). Surface temperature
160 increased from Anadyr Water (St. BS1, 3.2°C) to Alaskan Coastal Water (St. BS8, 10.8°C), and salinity
161 decreased from 33.0 (St. BS1) to 30.8 (St. BS8) (Fig. 2).

162



163
 164 **Fig. 2.** Temperature ($^{\circ}\text{C}$), salinity and Chlorophyll *a* ($\text{Chl } a$, $\mu\text{g L}^{-1}$) profiles from the surface to bottom
 165 (or 200 m). Black dots: sampling depths; black dotted box: different transects; black dashed line:
 166 boundary of the Bering Sea and Bering Strait.

167

168 3.2. Neritic tintinnid species composition

169 Nineteen neritic tintinnid species belonging to five genera were identified (Table 2; Appendix 1).

170 Among them, 15 species belonging to genus *Tintinnopsis*, which accounting for 78.9% of the total

171 neritic species richness. We classified nine species with maximum abundance ≥ 20 cells L^{-1} and percent

172 occurrence $> 10\%$ as abundant species (Table 2): *Helicostomella subulata*, *Leprotintinnus pellucidus*,

173 *Tintinnopsis baltica*, *T. brasiliensis*, *T. karajacensis*, *T. parva*, *T. parvula*, *T. rapa* and *T. tubulosoides*

174 (Table 2; Appendix 1). *Helicostomella subulata* had the highest maximum abundance (204 cells L^{-1}),

175 while *T. rapa* had the highest percent occurrence (40.1%) (Table 2). Other species were defined as rare

176 species.

177

178 **Table 2**

179 Summary of neritic tintinnid species in the shelf waters of Bering Sea and Chukchi Sea. LOD:

180 lorica oral diameter; A_{max} : maximum abundance; TSP: total number of samples where the species

181 was present; PO: percent occurrence; *: species with counting number < 10 . Species in red were

182 regarded as abundant species with maximum abundance ≥ 20 cells L^{-1} and percent occurrence $> 10\%$.

183 The LOD and Body length were presented into mean values \pm standard deviation. Abundant
 184 species and *Tintinnopsis fimbriata* were classified into neritic surface-/bottom- dwellers according
 185 to vertical distribution. Rare species, other than *T. fimbriata*, were classified into unclear group
 186 because of their low abundance and percent occurrence.

Group	Species	LOD (μm) (n=10)	Body length (μm) (n=10)	A _{max} (cells L ⁻¹)	TSP	PO (%)
Surface-dweller	<i>Helicostomella subulata</i>	22.3 \pm 0.9	225.8 \pm 36.0	204	60	30.5
	<i>Leprotintinnus pellucidus</i>	39.7 \pm 2.2	196.9 \pm 35.8	118	25	12.7
	<i>Tintinnopsis karajacensis</i>	32.3 \pm 1.9	86.5 \pm 7.4	20	42	21.3
	<i>T. tubulosoides</i>	32.5 \pm 1.4	81.7 \pm 14.3	74	47	23.9
Bottom-dweller	<i>Tintinnopsis baltica</i>	40.7 \pm 4.7	63.5 \pm 5.7	174	58	29.4
	<i>T. brasiliensis</i>	42.6 \pm 2.0	65.2 \pm 5.1	110	63	32.0
	<i>T. parva</i>	28.8 \pm 1.8	40.1 \pm 3.0	24	34	17.3
	<i>T. parvula</i>	23.6 \pm 1.8	48.8 \pm 3.7	27	31	15.7
	<i>T. rapa</i>	23.3 \pm 2.0	53.1 \pm 4.7	157	79	40.1
	<i>T. fimbriata</i>	53.9 \pm 3.5	70.3 \pm 2.7	18	9	4.6
Unclear	<i>Metacylis conica</i> *	15.1 \pm 1.2	57.7 \pm 4.2	10	4	2.0
	<i>Stenosemella ventricosa</i>	35.3 \pm 2.2	78.0 \pm 4.5	20	8	4.1
	<i>Tintinnopsis acuminata</i>	29.1 \pm 2.0	66.7 \pm 7.9	5	7	3.6
	<i>T. beroidea</i> *	22.4	45	1	1	0.5
	<i>T. glans</i>	25.6 \pm 3.0	36.5 \pm 5.2	20	16	8.1
	<i>T. levigata</i>	24.5 \pm 1.0	49.3 \pm 6.3	10	12	6.1
	<i>T. lohmanni</i> *	46.0 \pm 2.7	79.4 \pm 7.5	11	4	2.0
	<i>T. strigosa</i>	25.8 \pm 1.7	57.0 \pm 3.2	15	13	6.6
	<i>T. urnula</i>	30.6 \pm 2.2	58.3 \pm 4.7	107	19	9.6

187

188 3.3 Distribution of neritic tintinnids

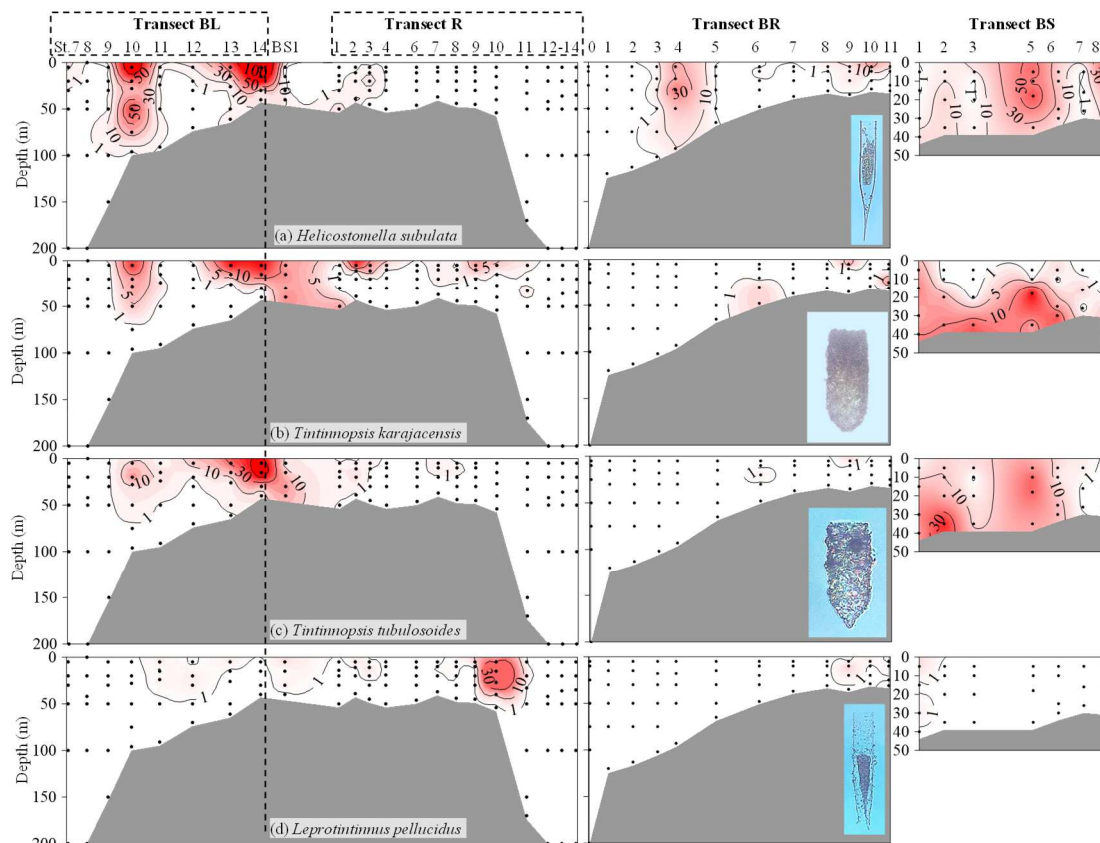
189 According to the vertical distribution, abundant neritic tintinnids were divided into
 190 surface-dwellers (high abundance (≥ 20 cells L⁻¹) mainly distributed in surface water (upper 10 m
 191 layers)) and bottom-dwellers (high abundance mainly distributed at depths near seafloor) (Figs. 3 and
 192 4).

193 3.3.1 Neritic tintinnid surface-dwellers

194 Four neritic tintinnid species (*Helicostomella subulata*, *Leprotintinnus pellucidus*, *Tintinnopsis*
 195 *karajacensis* and *T. tubulosoides*) belonged to this group (Fig. 3). High abundance of *H. subulata*
 196 appeared in all the Bering Sea shelf waters (Transects BL, BR and BS), but decreased northward from

197 the Bering Strait to Arctic Ocean (Fig. 3a). *Tintinnopsis karajacensis* and *T. tubulosoides* had high
 198 abundances in surface waters in Transect BL, but in Transect BS, they had high abundances in bottom
 199 waters (Fig. 3b, c). However, we considered them as surface-dwellers. *Leprotintinnus pellucidus*
 200 occurred in all Transects, while the highest abundance appeared at the north end of Transect R (Fig.
 201 3d).

202 All four species had higher abundances in Transect BL than in Transect BR (Fig. 3). In the
 203 Transect BS, *Helicostomella subulata* was distributed evenly throughout the three Pacific Inflow
 204 Waters (the Anadyr Water, Bering Shelf Water and Alaskan Coastal Water) (Figs. 2 and 3a), while *T.*
 205 *karajacensis*, *T. tubulosoides* and *L. pellucidus* mainly appeared in Anadyr Water (Figs. 2 and 3b-d).



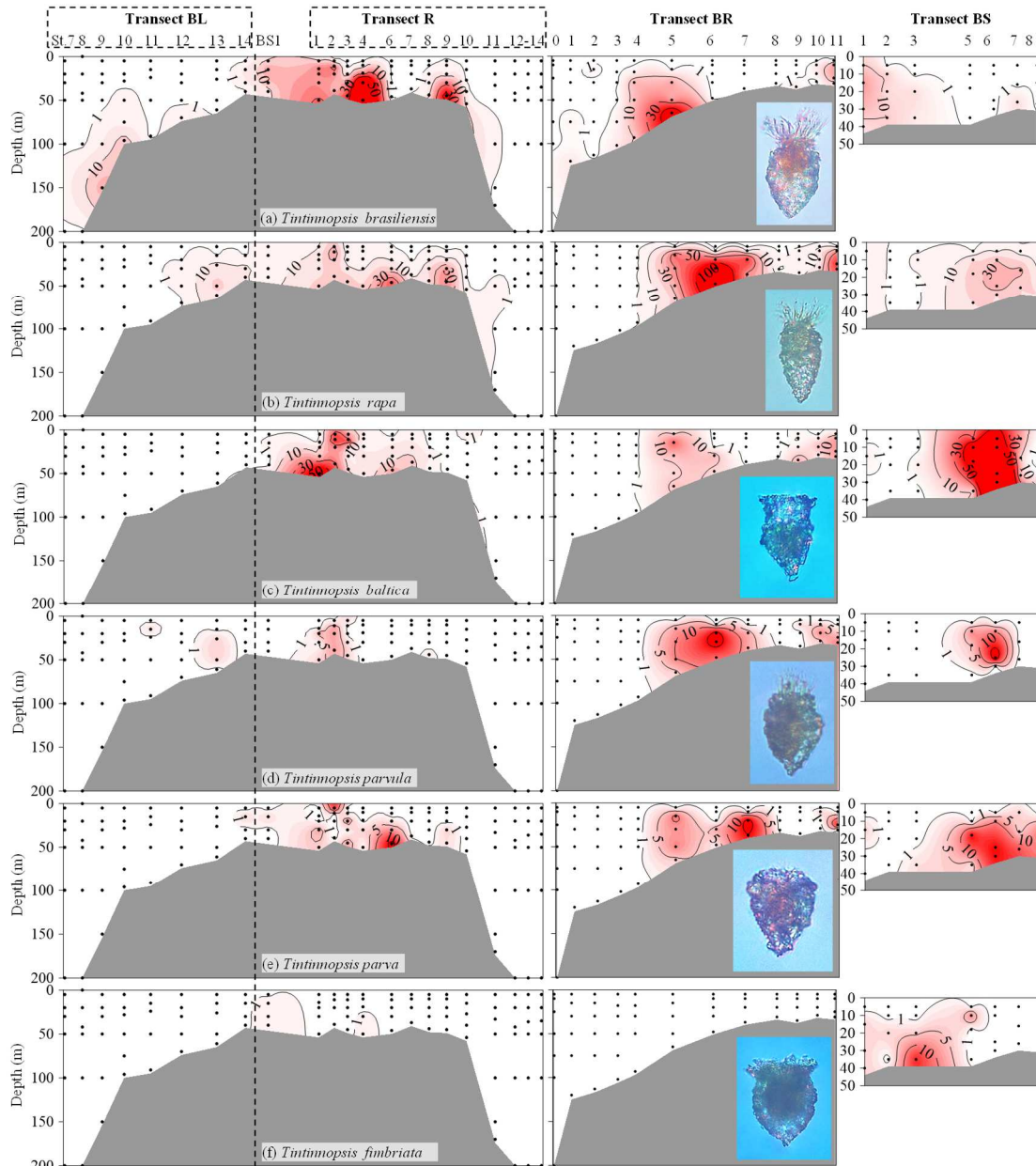
206
 207 **Fig. 3.** Abundances (cells L⁻¹) and vertical distributions of surface neritic tintinnid species from the
 208 surface to bottom (or 200 m). Black dots: sampling depths; black dotted box: different transects; black
 209 dashed line: boundary of the Bering Sea and Bering Strait.
 210

211 3.3.2 Neritic tintinnid bottom-dwellers

212 Five abundant neritic tintinnid species (*Tintinnopsis rapa*, *T. brasiliensis*, *T. baltica*, *T. parvula*
213 and *T. parva*) belonged to this group (Fig. 4a-e). High abundance of above species mainly located in
214 the Bering Strait and adjacent seas. Although *T. fimbriata* was not an abundant neritic tintinnid species,
215 high abundance of this species occurred in bottom layers (Fig. 4f). Thus this species also belonged to
216 neritic tintinnid bottom-dwellers.

217 The distribution range of each above species was different in the two transects (BL and BR) of the
218 Bering Sea. Among them, *T. brasiliensis* had the largest distribution range (Fig. 4a). This species had
219 high abundance in both Transects BL and BR. While for *T. rapa*, *T. baltica*, *T. parvula* and *T. parva*,
220 high abundance of these species only occurred in Transect BR (Fig. 4b-e). *T. fimbriata* only appeared in
221 the Bering Strait (Fig. 4f).

222 In the Transect BS, five abundant species and *T. fimbriata* distributed in different Pacific Inflow
223 Waters (Figs. 2 and 4). *T. brasiliensis* (Fig. 4a) and *T. fimbriata* (Fig. 4f) mainly distributed in western
224 side of the transect BS, where the locations corresponding to the Anadyr Water (Figs. 1 and 2). While
225 other four abundant species (*T. rapa*, *T. parvula*, *T. parva* and *T. baltica*) mainly occurred in eastern
226 side of the transect BS, where the locations corresponding to the Bering Shelf Water (Figs. 1 and 2).



228

229 **Fig. 4.** Abundances (cells L⁻¹) and vertical distributions of bottom neritic tintinnid species from the
 230 surface to bottom (or 200 m). Black dots: sampling depths; black dotted box: different transects; black
 231 dashed line: boundary of the Bering Sea and Bering Strait.

232 3.3.3 Rare neritic tintinnid species

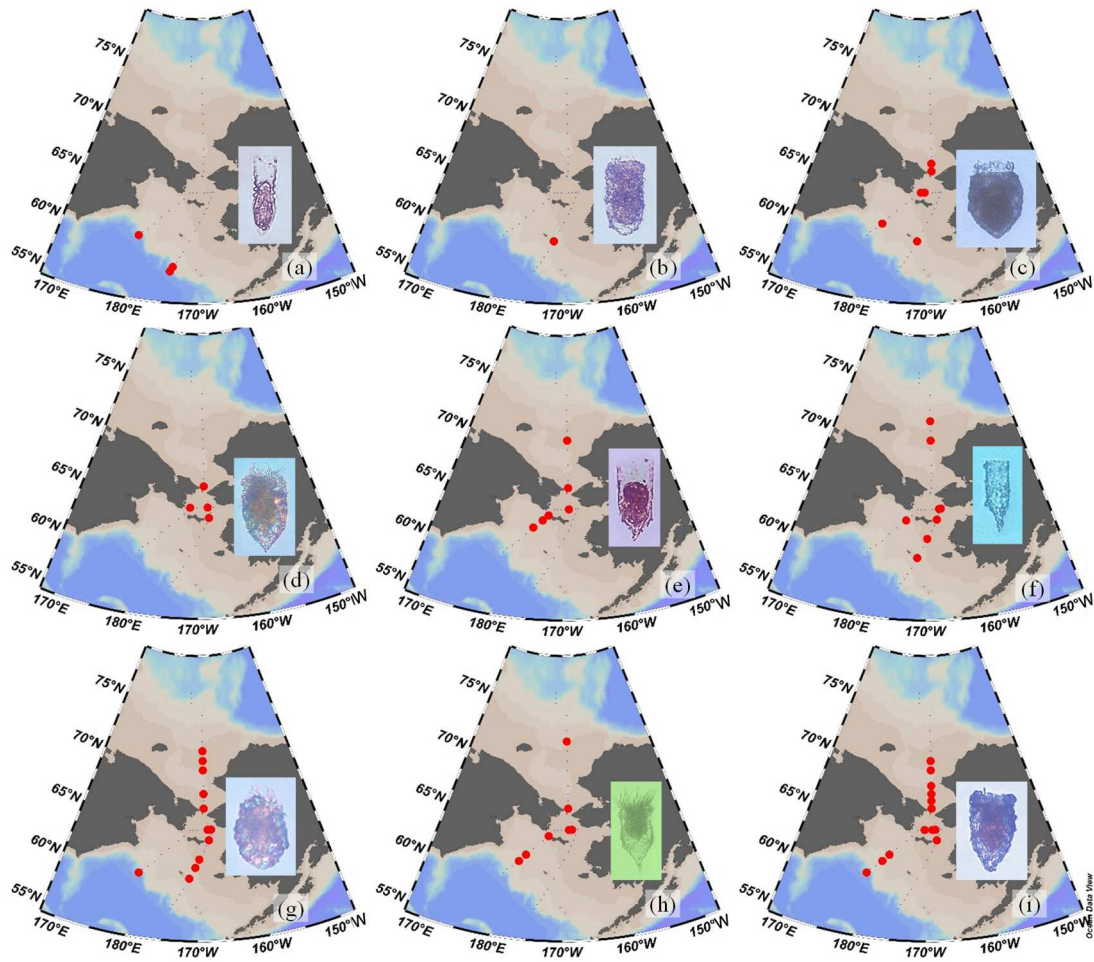
233 The nine rare species were divided into three patterns according to their distribution ranges:

234 pattern I: *Metacylis conica*, *T. beroidea* and *Stenosemella ventricosa* mainly appeared in the Bering Sea

235 (Fig. 5a-c); pattern II: *T. lohmanni* mainly occurred in the Bering Strait (Fig. 5d); and pattern III: *T.*

236 *acuminata*, *T. levigata*, *T. glans*, *T. strigosa* and *T. urnula* appeared in the Bering Sea, the Bering Strait

237 and the Chukchi Sea shelf water (Fig. 5e-i; Appendixes 1 and 2). There were no neritic species that
 238 occurred in only the Chukchi Sea shelf water. High abundances of most rare neritic tintinnid species
 239 occurred in waters shallower than 100 m. In Transect BS, the rare tintinnid species had higher
 240 abundances in Bering Shelf Water than in either Anadyr Water or Alaskan Coastal Water (Appendix 2).
 241



242
 243 **Fig. 5.** Horizontal distribution of rare neritic tintinnid species. (a) *Metacylis conica*; (b) *Tintinnopsis*
 244 *beroidea*; (c) *Stenosemella ventricosa*; (d) *T. lohmanni*; (e) *Tintinnopsis acuminata*; (f) *T. levigata*; (g) *T.*
 245 *glans*; (h) *T. strigosa* and (i) *T. urnula*. Red dots means occurrence stations.

246

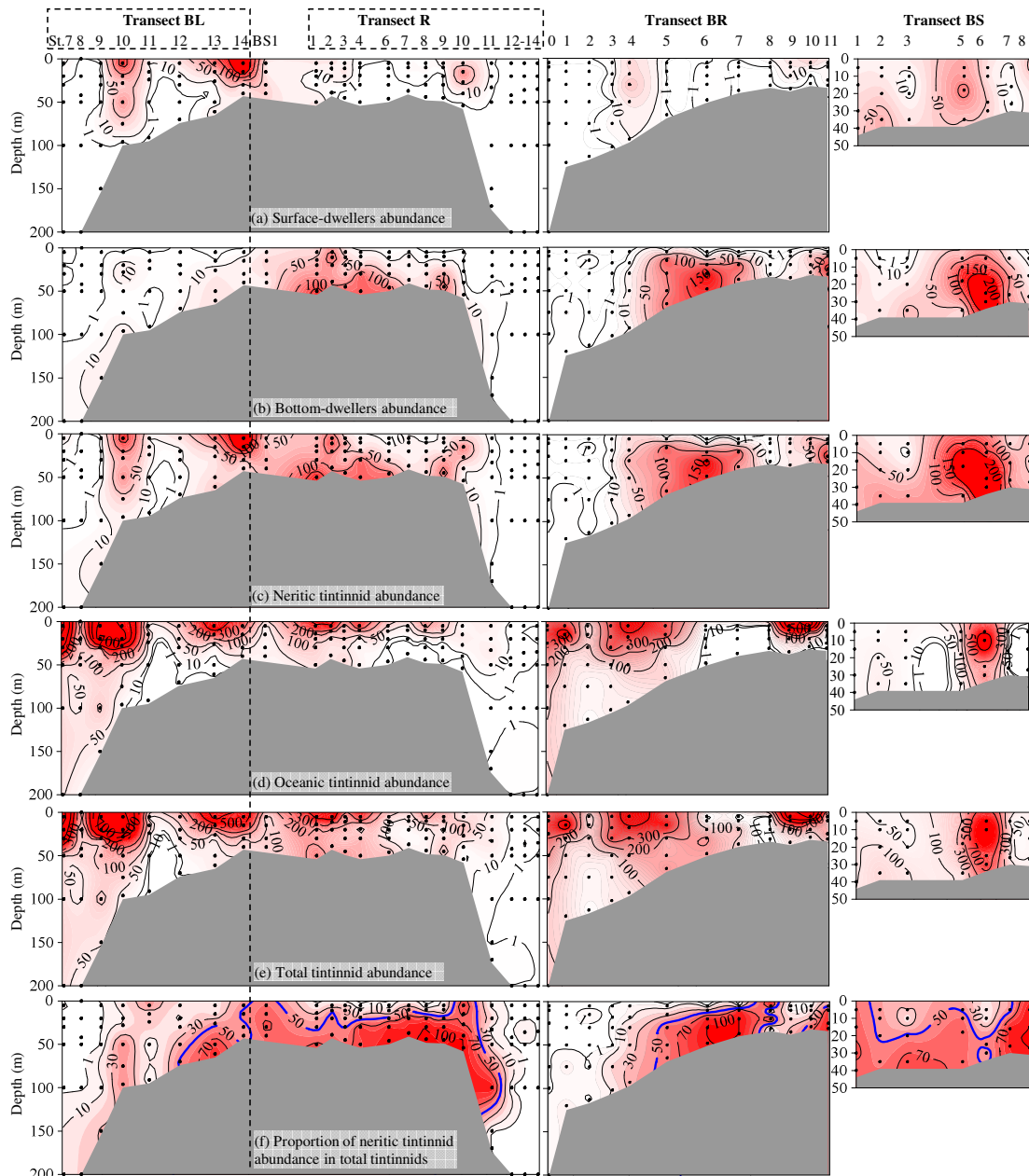
247 3.4 Mixing of the neritic and oceanic tintinnids

248 Neritic tintinnid total abundance ranged from 0 to 437 cells L⁻¹. Among them, neritic
 249 surface-dweller and bottom-dweller abundances ranged from 0 - 287 cells L⁻¹ and from 0 - 389 cells L⁻¹,
 250 respectively. In Transect BL, surface-dwellers were more abundant than bottom-dwellers, but opposite

251 in Transect BR (Fig. 6a and 6b). Bottom-dwellers abundance was low in the surface waters of the
252 Bering Sea and Bering Strait (Fig. 6b). In Transect BS, neritic species exhibited a higher total
253 abundance in Bering Shelf Water (Sts. BS5 and BS6) than in either Anadyr Water or Alaskan Coastal
254 Water (Figs. 2 and 6c).

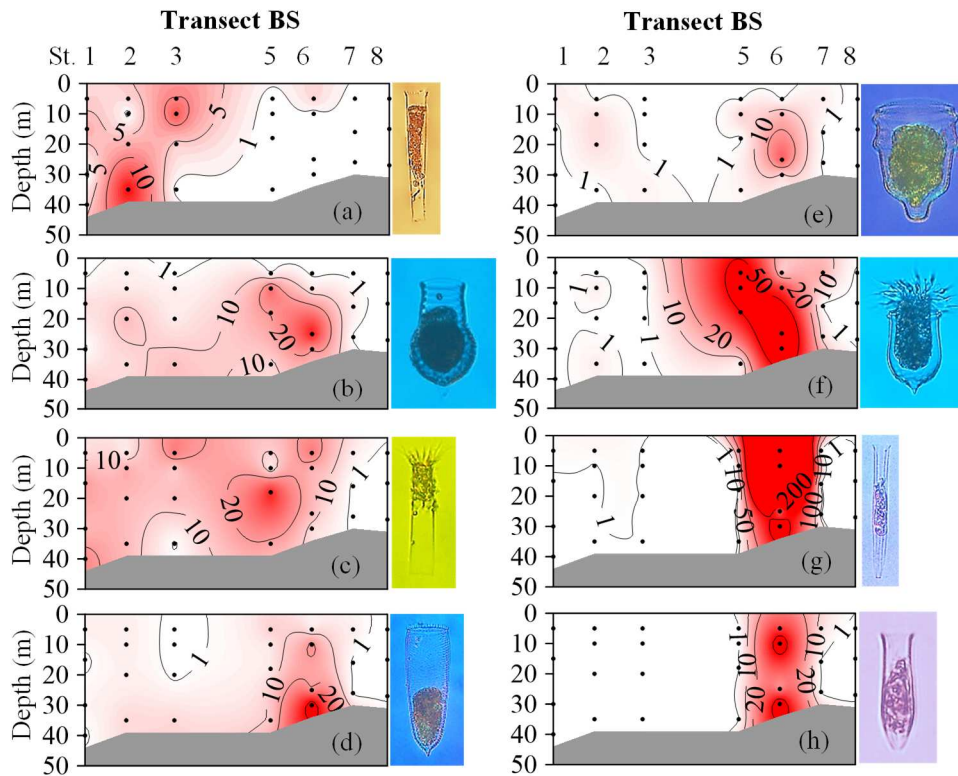
255 Oceanic tintinnid abundance ranged from 0 to 1568 cells L⁻¹. High abundance (> 100 cells L⁻¹)
256 occurred in the upper 50 m of the water column, alongside the 5 °C isotherm and 32.5 isohaline (Figs.
257 2 and 6d). Eight oceanic tintinnid species (*Eutintinnus pectinis*, *Codonellopsis frigida*, *Eutintinnus* sp.1,
258 *Parafavella* spp., *Ptychocylis obtusa*, *Acanthostomella norvegica*, *Salpingella* sp.1 and *Salpingella* sp.2)
259 were observed in Transect BS (Fig. 7). Except for *Eutintinnus pectinis*, which mainly appeared in
260 Anadyr Water (Fig. 7a), the other species were more abundant in Bering Shelf Water (Sts. BS5 and BS6)
261 than in either Anadyr Water or Alaskan Coastal Water (Fig. 7b-h). Maximum abundances of
262 *Acanthostomella norvegica* (80 cells L⁻¹), *Salpingella* sp.1 (1405 cells L⁻¹) and *Salpingella* sp. 2 (67
263 cells L⁻¹) exceeded 50 cells L⁻¹ (Fig. 7f-h).

264 Total tintinnid abundance ranged from 0 to 1723 cells L⁻¹ from the Bering Sea to the Chukchi Sea
265 (Fig. 6e). The majority of shallow water stations (< 150 m depth) were dominated by neritic tintinnids
266 (abundance proportion to the total tintinnid abundance was higher than 50%) in bottom layers (Fig. 6f).



267

268 **Fig. 6.** Tintinnid abundances (cells L⁻¹) (a-e) and proportion (%) of neritic tintinnid abundance in total
 269 tintinnids (f) from the surface to bottom (or 200 m). Black dots: sampling depths; black dotted box:
 270 different transects; black dashed line: boundary of the Bering Sea and Bering Strait.



271

272 **Fig. 7.** Abundances (cells L⁻¹) and vertical distribution of oceanic species (a: *Eutintinnus pectinis*, b:
 273 *Codonellopsis frigida*, c: *Eutintinnus* sp.1, d: *Parafavella* spp., e: *Ptychocylix obtusa*, f:
 274 *Acanthostomella norvegica*, g: *Salpingella* sp.1, h: *Salpingella* sp.2) from the surface to bottom in
 275 transect BS. Black dots: sampling depths.

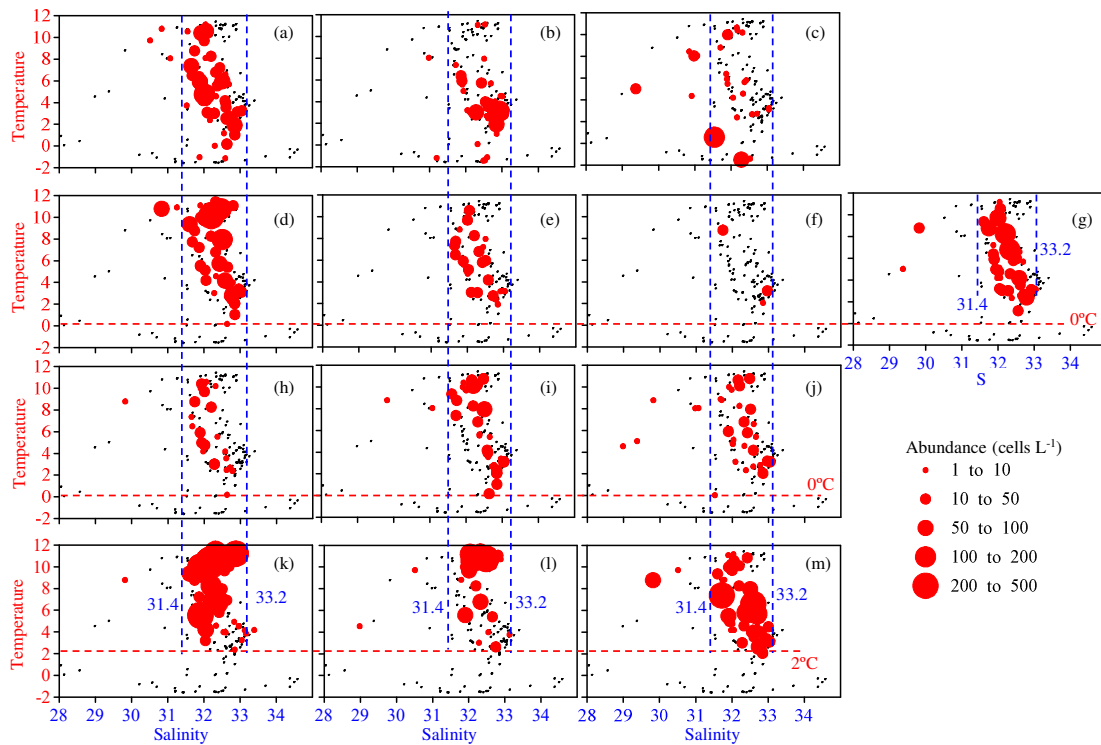
276

277 3.5 Relationship between neritic tintinnid species abundances and environmental factors

278 Temperature-salinity-plankton diagrams showed that nine abundant neritic species had different
 279 temperature and salinity ranges (Fig. 8). *Tintinnopsis rapa*, *T. brasiliensis* and *L. pellucidus* had wider
 280 temperature range (-1.8 - 11.8°C; Fig. 8a-c) than other neritic species (*H. subulata*, *T. parva*, *T.*
 281 *fimbriata*, *T. baltica*, *T. parvula*, *T. tubulosoides* and *T. karajacensis*) in warm waters > 0°C (Fig. 8d-j).
 282 All abundant neritic species were present at salinity ranging from 31.4 to 33.2 (Fig. 8a-j).

283 Three oceanic tintinnid species (*Salpingella* sp.1, *Salpingella* sp.2 and *Eutintinnus* sp.1) were not
 284 analyzed or found in Wang et al. (2019). These three oceanic species had a similar salinity range (from
 285 31.4 to 33.2) but a narrower temperature range (from 2°C to 12°C) compared to neritic tintinnid species
 286 (Fig. 8k-m). Among them, high abundance of *Salpingella* sp.1 was consistent with high temperatures

287 (Fig. 8k). *Salpingella* sp.2 (the same species as the “undetermined species” of Li et al. (2016a) and
 288 Wang et al. (2019)) was more abundant at temperature > 8°C than at temperature 2-8°C (Fig. 8l).
 289 However, *Eutintinnus* sp. 1 was in lower abundance at temperature > 8°C than at temperature <
 290 8°C (Fig. 8m).



291
 292 **Fig. 8.** Temperature (°C) and salinity ranges of neritic (a-j) and oceanic (k-m) tintinnid species. a:
 293 *Tintinnopsis rapa*; b: *T. brasiliensis*; c: *Leprotintinnus pellucidus*; d: *Helicostomella subulata*; e:
 294 *T. parva*; f: *T. fimbriata*; g: *T. baltica*; h: *T. parvula*; i: *T. tubulosoides*; j: *T. karajacensis*; k: *Salpingella*
 295 sp.1; l: *Salpingella* sp.2; m: *Eutintinnus* sp.1. Black dots: sampling depths.

296

297 Different neritic tintinnid species had different correlations with environmental factors
 298 (temperature, salinity and Chl *a*) (Table 3). *Helicostomella subulata* and *T. brasiliensis* had significant
 299 positive and negative correlations with temperature, respectively. *Tintinnopsis brasiliensis* and *T.*
 300 *fimbriata* had positive correlations and *L. pellucidus* had a negative correlation with salinity. Except *T.*
 301 *fimbriata*, all abundant neritic tintinnid species had positive correlations with Chl *a* (Table 3).

302

303 **Table 3**

304 Spearman's rank correlation between neritic tintinnids (9 dominant species and *Tintinnopsis fimbriata*)
 305 abundance (cells L⁻¹) and the temperature (°C), salinity and the Chl *a* (µg L⁻¹). **: $p < 0.01$; *: $p < 0.05$.

Species	Temperature	Salinity	Chl <i>a</i>
<i>Helicostomella subulata</i>	0.247**	-0.020	0.239**
<i>Leptotintinnus pellucidus</i>	0.034	-0.225**	0.146*
<i>Tintinnopsis baltica</i>	0.067	-0.109	0.403**
<i>T. brasiliensis</i>	-0.290**	0.305**	0.141*
<i>T. fimbriata</i>	-0.099	0.159*	0.100
<i>T. karajacensis</i>	0.127	-0.116	0.205**
<i>T. parva</i>	0.030	-0.054	0.162*
<i>T. parvula</i>	0.057	-0.107	0.235**
<i>T. rapa</i>	-0.052	-0.037	0.310**
<i>T. tubulosoides</i>	0.099	0.047	0.210**

306

307 **4. Discussion**308 **4.1 Neritic tintinnid composition and distribution in the Arctic and Pacific shelves**

309 Tintinnid species composition and vertical distribution are also observed in other regions of the
 310 Arctic Ocean and adjacent seas (e.g., Lovejoy et al., 2006; Simo-Matchim et al., 2017; Kršinić 2018;
 311 Wang et al., 2019, 2022). However, most previous tintinnid studies on the Arctic shelf and adjacent
 312 northern waters presented neritic tintinnid species lists (Boltovskoy et al., 1995; Dolan et al., 2017;
 313 Chovgan, 2019), but information on species abundance was very scarce. In this study, *Metacylis conica*,
 314 which was observed in the Bering Sea but not in the Chukchi Sea, had not been previously observed in
 315 Arctic shelf waters. Among the other 18 neritic tintinnid species that occurred in the Chukchi Sea shelf
 316 waters found in our study, thirteen had also been reported previously in other Arctic seas (Appendix 3).
 317 Five species (*T. brasiliensis*, *T. glans*, *T. levigata*, *T. parva* and *T. strigosa*) found on the Chukchi Sea
 318 shelf were recorded in Arctic shelf seas for the first time in our study.

319 Latitudinally, high abundance of nine abundant species (*Tintinnopsis rapa*, *T. brasiliensis*,
 320 *Leptotintinnus pellucidus*, *Helicostomella subulata*, *T. parva*, *T. baltica*, *T. parvula*, *T. tubulosoides* and
 321 *T. karajacensis*) and *T. fimbriata* mainly occurred in the Bering Strait, which were different with

322 oceanic species (highest abundance in the Bering Sea and decreased northward) in Wang et al. (2019).
323 As for neritic tintinnid species, all 19 species in our results were also reported in oceans south
324 (Jiaozhou Bay (China), northern South China Sea, Pearl River Estuary (China), Sea of Okhotsk and
325 tropical western Pacific) of the Bering Strait (Appendix 3). These observations strongly suggest that
326 there were no endemic species in the Chukchi Sea in our research, and neritic tintinnids in the Bering
327 Sea and Chukchi Sea belonged to the same assemblage.

328 We found that all neritic tintinnid species had a relatively narrow salinity range (31.4 - 33.2) but a
329 wide temperature range (-1.8 - 11.8°C). This phenomenon was consistent with results related to the
330 subarctic oceanic assemblage in the Bering Sea (Wang et al., 2019).

331 **4.2 Differences for tintinnid in different water masses of Pacific Inflow Water in the Bering Strait**

332 Our study showed that both neritic and oceanic tintinnids had higher abundances in Bering Shelf
333 Water than in either Anadyr Water or Alaskan Coastal Water along Transect BS. There is no previous
334 report on the difference in tintinnids among these three water masses. Our result is consistent with
335 Springer et al. (1989), who found different zooplankton communities in different water masses of PIW.
336 Contrary to the highest zooplankton abundance in Anadyr Water (Springer et al., 1989), our study
337 showed higher tintinnid abundance in Bering Shelf Water. There might be two reasons for this
338 phenomenon. The first one was hydrographic features. Compared to Bering Shelf Water, Anadyr Water
339 was characterized with low temperature and Alaskan Coastal Water was characterized with low salinity
340 (Coachman et al., 1975; Liu et al., 2016), which might be unsuitable for tintinnids survival. The second
341 one was food item. The Bering Shelf Water had higher Chl *a* concentrations than Anadyr Water (Fig. 2),
342 which could provide sufficient food items to maintain tintinnid high abundance.

343 Oceanic tintinnids had a higher abundance in Bering Shelf Water than in either Anadyr Water or

344 Alaskan Coastal Water along Transect BS. Wang et al. (2019) found that the Pacific oceanic species
345 disappeared gradually along Transect R (170 °W), a repeated transect from Bering Strait to Arctic
346 Basin in most CHINARE cruises that is located west of Bering Shelf Water and Alaskan Coastal Water.
347 Therefore, these Pacific with oceanic tintinnids might intrude farther northward through Bering Shelf
348 Water and Alaskan Coastal Water than in Transect R, as in Wang et al. (2019).

349 **4.3 Neritic tintinnid vertical distribution and mixing with oceanic tintinnid**

350 Our study showed that neritic tintinnids were divided into surface- and bottom-dwellers. Previous
351 studies had no information about the vertical distribution of neritic tintinnids in the shelf water of
352 Bering Sea and Chukchi Sea. In fact, there were very few data about the vertical distribution of neritic
353 tintinnid species in Arctic shelf waters, except for two references in the Svalbard (Feng et al., 2014)
354 and Barents Sea (Boltovskoy et al., 1991). The surface-dwelling characteristics of *H. subulata*, *L.*
355 *pellucidus* and *T. tubulosoides* in our study were consistent with previous studies (Paranjape, 1987;
356 Boltovskoy et al., 1991). *Leprotintinnus pellucidus* was present in high abundance in the upper 25 m in
357 the Barents Sea (Boltovskoy et al., 1991) and Bedford Basin out of the Arctic (Paranjape, 1987). The
358 abundances of *H. subulata* and *T. tubulosoides* in the Bedford Basin also showed surface-peak pattern
359 (Paranjape, 1987). Vertical distribution data for *T. karajacensis* are not available in the literature. As for
360 neritic bottom-dwellers, they could still be found in surface waters above the thermocline in Bering Sea
361 and Chukchi Sea, although in low abundance. This phenomenon might due to upwelling caused by
362 Pacific Inflow Water flow over shelves (Woodgate et al., 2005; Zhao et al., 2006).

363 The total abundance of neritic tintinnids was low compared with that of oceanic tintinnids. The
364 abundance proportion of neritic tintinnid species was $\leq 50\%$ in surface waters. Combining literature
365 (Woodgate et al., 2005; Zhao et al., 2006) with water temperature and salinity vertical distribution

366 characteristics in our results, we speculated that wind-induced currents produced upwelling in the
367 Bering Strait might be the main reason to explain neritic and oceanic tintinnids mixing in water column.
368 The large contribution of Pacific plankton to Bering Sea and Chukchi Sea plankton was also reported
369 by Springer et al. (1989). Oceanic tintinnids were mainly present above the thermocline in our study as
370 well as in Wang et al. (2019), indicating that the intruding oceanic tintinnids had more influence on
371 neritic surface-dwellers than on bottom-dwellers. Thus, in the study area, the surface waters were
372 mainly occupied by intruding oceanic communities.

373 **4.4 Possible response of the tintinnid community to increasing Pacific Inflow Water**

374 Because of global warming and the increasing trend of PIW (Woodgate, 2018), the Pacific-Arctic
375 Ocean are experiencing pacification (The anomalous influx of Pacific waters creating conditions
376 favorable for increased heat and freshwater content in the Beaufort Gyre halocline and expansion of
377 Pacific species into the Arctic interior) (Polyakov et al., 2020). The proportion of neritic tintinnids
378 might decrease, especially in the surface waters above the thermocline. After entering the Canada Basin,
379 PIW will sink into subsurface layers (approximately 50 m to 100 m depth), named as Pacific halocline
380 water (Steele et al., 2004; Zhong et al., 2019). Neritic species might die out in Pacific halocline water
381 due to their neritic nature. Oceanic species might live for some time as expatriate due to the so-called
382 trail of death effect (Wassmann et al., 2015). In the Canada Basin, *Ptychocylis urnula* was the dominant
383 Arctic species with high abundances in surface and deep Chlorophyll *a* maximum (DCM) layers.
384 Between the two layers of *Ptychocylis urnula*, there were no oceanic species originated from the PIW
385 (Wang et al., 2019). We speculate that with the progress of global warming, the living time of oceanic
386 species from PIW will last for a longer time in Pacific halocline water of the Arctic Ocean.

387 For the first time in the Bering Strait, two oceanic tintinnid species (*Eutintinnus* sp.1 and

388 *Salpingella* sp.1) were observed along Transect BS. In the Bering Sea and the Bering Strait, *Salpingella*
389 sp.2 was reported in low abundance ($A_{\max}=12$ cells L^{-1}) in 2016 (Wang et al., 2019), but this species
390 was dominant ($A_{\max} = 517$ cells L^{-1}) in the Bering Shelf Water in present study. These oceanic
391 tintinnids originated from the Bering Sea (*Acanthostomella norvegica*, *Salpingella* sp.1 and *Salpingella*
392 sp.2) might be found in Pacific halocline water in future investigations as a consequence of global
393 warming.

394

395 **5. Conclusions**

396 In this study, neritic tintinnid species richness, vertical distribution, mixing with oceanic tintinnids
397 and correlation with environmental factors from the Bering Sea shelf to the Chukchi Sea shelf were
398 investigated. We found 19 neritic tintinnid species belonging to 5 genera in the Pacific Arctic Region.
399 Abundant neritic species appeared in both the Bering Sea and the Chukchi Sea shelves. According to
400 vertical distribution of high abundance, abundant neritic tintinnids were divided into surface- and
401 bottom-dwellers, respectively. In Pacific Inflow Water, both neritic and oceanic tintinnid community
402 compositions were different from the western to eastern side of Bering Strait (Transect BS). Neritic
403 tintinnids showed vertical mixing patterns with oceanic tintinnids present in the upper layer above the
404 thermocline. All abundant neritic tintinnid species lived within a similar salinity range (31.4 - 33.2) but
405 a wide temperature range (-1.8 - 11.8°C). With the increasing trend of PIW, more neritic and oceanic
406 tintinnids in Bering Shelf Water might be transported into the Canada Basin, where some of them
407 might be found in the future as a consequence of global warming.

408

409 **CRedit authorship contribution statement**

410 **Chaofeng Wang:** Conceptualization, Methodology, Software, Data Curation, Writing - Original
411 Draft, Funding acquisition. **Zhiqiang Xu:** Software, Data Curation, Funding acquisition. **Yan He:**
412 Investigation, Software. **Chao Yuan:** Investigation, Software. **Haibo Li:** Methodology, Software.
413 **Yuan Zhao:** Writing - Review & Editing, Supervision. **Michel Denis:** Writing - Review & Editing.
414 **Wuchang Zhang:** Conceptualization, Investigation, Writing - Review & Editing, Supervision, Project
415 administration. **Tian Xiao:** Project administration.

416

417 **Declaration of competing interest**

418 The authors declare that they have no known competing financial interests or personal
419 relationships that could have appeared to influence the work reported in this paper.

420

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428

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