

[Click here to view linked References](#)

1 **Cross-shelf structure and distribution of mesozooplankton communities in the East-**
2 **Siberian Sea and the adjacent Arctic Ocean**

3 E. A. Ershova^{1,2*}, K. N. Kosobokova²

4 ¹UiT The Arctic University of Norway, Faculty for Biosciences, Fisheries and Economics, Department for Arctic and Marine
5 Biology, 9037 Tromsø, Norway; ²Shirshov Institute of Oceanology, Russian Academy of Sciences, 36 Nakhimova Avenue,
6 117997 Moscow, Russian Federation

7
8 *Correspondence:

9 Elizaveta Ershova

10 elizaveta.ershova@uit.no

11

12 **Abstract** The East-Siberian Sea (ESS) plays a significant role in circulation of the surface
13 water and biological production in the Arctic, yet due to its remote location and historically
14 difficult sampling conditions remains the most understudied of all Arctic shelf seas, with
15 even baseline information on biological communities absent in literature. We contribute to
16 such a baseline by describing the distribution and community structure of
17 mesozooplankton in the ESS and the adjacent Arctic Ocean based on recent (September
18 2009, 2015) as well as historical (August-September 1946, 1948) data. We found that the
19 overall biomass and abundance during our studies were significantly lower than in the
20 adjacent Chukchi Sea, but higher than historical estimates from ESS, around 25-35 mg DW
21 m⁻³. The diversity was low and characteristic for other Arctic shelf seas, with increasing
22 number of species in deeper waters. Biomass was highest at the shelf break, where it
23 approached 70 mg DW m⁻³, and was mainly composed of the large copepod *Calanus*
24 *glacialis*. On the shelf, abundance and biomass were low (10-20 mg DW m⁻³) and dominated
25 by small copepods and chaetognaths. Several distinct assemblages of zooplankton were
26 identified and related to the physical properties of the water masses present. A striking
27 result was the presence of both Atlantic and Pacific expatriates in offshore waters close to
28 the shelf break, but generally not on the shelf. Tracking these advected organisms could be
29 a useful tool in determining the pathways, extent and transit time of Atlantic and Pacific
30 water entering the Arctic.

31

32 **Keywords:** Arctic Ocean, zooplankton, pelagic ecosystems, climate change

33 **Introduction**

34 The East-Siberian Sea (ESS) is located east of the Laptev Sea and west of the Chukchi
35 Sea, bordered by the New Siberian Islands on the west and Wrangel Island on the East (Fig.
36 1). It is the largest, broadest and shallowest of all Arctic shelf seas, widely open to the Arctic
37 Basin. Nearly 70% of the shelf of the ESS is shallower than 50 m, with most of the area
38 dominated by depths of 20–25 m (Williams and Carmack 2015). Oceanographically, it
39 interacts both with the adjacent Atlantic-influenced Laptev Sea, and the Pacific-influenced
40 Chukchi Sea and is heavily influenced by river runoff from large Siberian rivers Kolyma and
41 Indigirka (Semiletov et al. 2005). The water exchange between the ESS and neighboring
42 Laptev and Chukchi Seas is mostly determined by atmospheric circulation varying
43 significantly year to year. Eastward winds keep riverine water from the Laptev Sea close to
44 the coast and lead to the development of the Siberian Coastal Current, which carries low
45 salinity water eastward through the Long Strait into the Chukchi Sea. In contrast, prevailing
46 westward winds cause fresh surface water to be transported off the shelf, and the direction
47 of the prevailing currents is reversed, resulting in advection of Pacific-origin water from
48 the Chukchi Sea (Weingartner et al. 1999). Historically, the ESS has been the most heavily
49 ice-covered shelf within the Eurasian Arctic, characterized by extensive pack ice formation
50 that reached 300-500km from the shore (Dobrovolskii and Zalogin 1982).

51 Despite much effort being devoted to Arctic research in recent decades, mostly it has
52 been concentrated in relatively easily accessible regions within the European and north-
53 American sectors (e.g. Kassens et al. 1999; Stein et al. 2003; Flint et al. 2010; Grebmeier
54 and Maslowski 2014). The large knowledge gaps remain primarily along the Siberian shelf,
55 despite its high significance for sea ice formation and ocean circulation within the Arctic.
56 Due to its remote location, shallow depths inaccessible to large research vessels, and
57 historically severe ice conditions, the ESS remains the most understudied of all Arctic
58 shelves, even compared to other Russian Arctic seas, with the few existing studies in
59 western literature limited to oceanography and biogeochemistry (i.e., Münchow et al.
60 1999; Semiletov et al. 2005; Anderson et al. 2011; Pipko et al. 2011). Limited information
61 on the East Siberian shelf pelagic biological communities collected in the 1940's, and
62 1980's was published in Russian "grey" literature (Brodsky 1957; Pavshchikov 1994; Pinchuk

63 1994). It is not easily accessible even in Russian, and unavailable in English. No published
64 zooplankton studies have been conducted in this region since 1986.

65 As the sea ice extent, duration and thickness continues to decline in the Arctic, it has
66 become common in recent years for the entire East-Siberian shelf to become ice-free
67 during the ice minimum (Nghiem et al. 2006; Kwok et al. 2009). Similar to other areas of
68 the Arctic (Buchholz et al. 2012; Ershova et al. 2015a; Vihtakari et al. 2018), this is
69 expected to result in significant shifts in plankton production patterns and community
70 composition. In order to be able to detect the ongoing changes in the pelagic ecosystem of
71 this region, within this study we aimed to provide baseline information on the structure of
72 the ESS zooplankton communities using net-based data collected in the ESS and adjacent
73 Arctic Ocean in September 2015. We also complement our data with other available
74 datasets collected on the ESS shelf: 2009, when the area was similarly nearly ice-free, and
75 August-September 1946-1948, when it was covered with pack ice (Pavshtiks 1994). This is
76 the first study in western literature providing description of the species composition,
77 spatial distribution, abundance, biomass estimates and community structure analysis of the
78 ESS zooplankton.

79

80 **Methods**

81 *Zooplankton collection and processing*

82 Zooplankton samples were collected in September 2015 from the R/V “Akademik
83 Tryoshnikov” at 16 stations in the northern ESS, on two transects extending from the shelf
84 (~35m depth) onto the basin (>2000m) (Fig. 1). Mesozooplankton was collected using a
85 closing Juday net with a mesh size of 180 μm and opening diameter of 37 cm. At each
86 station, stratified samples were taken at depth intervals of ~0-25, 25-65, 65-130, 130-260,
87 and 260-450 m. No samples were collected deeper than 450 m due to the limitations of the
88 research vessel. The net was towed vertically with a wire speed of 0.5 m/sec, and closed at
89 each designated depth with a messenger, which was propelled down the wire as the net
90 ascended. The volume of the water sampled was calculated from the height of each tow;
91 100% filtering efficiency was assumed, as there were no observed cases of clogging of the
92 nets. Zooplankton samples were preserved using 10% formalin (4% formaldehyde) for
93 later processing in the laboratory.

94 In the laboratory, each sample was scanned under stereomicroscope for large and
95 uncommon species, which were identified to the lowest taxonomic level and measured. The
96 rest of the sample was split using a Folsom splitter until there were ~100 individuals of the
97 most common species in the terminal split. Increasingly larger splits were scanned to
98 obtain counts for rarer taxa; a total of 400-600 individuals were examined from each
99 sample. All organisms were measured using a computer measurement system (ZoopBiom
100 software, Roff and Hopcroft 1986) and the DW of each specimen was predicted from a
101 length-weight regression relationship known for the same species, or a morphologically
102 similar organism (Ershova et al. 2015b). Copepods were staged and identified to species;
103 copepodite stages within some genera, which are morphologically undistinguishable (i.e.
104 *Pseudocalanus* spp.) were pooled together by stage. Meroplankton was grouped to the
105 macrotaxa or to the family level (in the case of shrimp larvae).

106

107 *Sea ice conditions, oceanography and Chlorophyll-a*

108 Sea ice concentrations were obtained for each sampling location from the Nimbus-7
109 SMMR and DMSP SSM/ISSMIS Passive Microwave Data set, available through the NSIDC
110 archives (Cavalieri et al. 1996). In addition to sea ice concentration, the distance to the
111 nearest ice edge, defined as 15% ice concentration, was calculated for each station (with
112 positive values indicating open water stations, and negative values indicating ice-covered
113 stations). Temperature and salinity data were collected with a Seabird SBE911plus CTD
114 system (SeaBird™ Electronics Inc.) equipped with a dissolved oxygen sensor,
115 transmissometer, fluorometer, and turbidity sensor with data binned into 1-m intervals
116 during post processing. The water column was divided into water masses based on the
117 definitions for the Arctic Ocean in Rudels (2008). Chlorophyll samples were collected using
118 Niskin bottles attached to the CTD casts at depths approximately corresponding to 3, 10,
119 20, 30, 40 and 50 meters. Typically, 500 ml of sample water was filtered onto GF/F glass
120 fiber filters, extracted in 90% acetone and analyzed fluorometrically. All samples were
121 processed at sea.

122

123 *Comparison to other datasets*

124 Our data on zooplankton distribution was compared to published and unpublished data
125 from other expeditions collected during the same time period (September) in 2009
126 (Ershova et al. 2015b), as well as 1946 and 1948. The 1946 data, collected from the Soviet
127 ice-breaking vessel “Temp”, is found in a brief publication about ESS zooplankton by
128 Pavshchikov (1994); the 1948 data, sampled from the ice-breaker “Severnyj Poljus” in the
129 Chukchi and East-Siberian Sea, is available from an archive compiled for the Arctic regions
130 by Markhaseva et al. (2005). To our knowledge, this joint dataset represents all publically
131 available zooplankton data for this region, with the exception of the expedition to Chaun
132 Bay in 1986 (Pinchuk, 1994). The latter was excluded due to being restricted only to the
133 inner bay and not extending onto the shelf. The listed expeditions have little spatial
134 overlap (Fig. 1), but together cover a wide area of the ESS shelf. The samples during the
135 2009 expedition were collected by a 150- μ m double ring net of 60-cm mouth diameter,
136 with flowmeters attached at the mouth, towed vertically from \sim 5 m off the seafloor to the
137 surface at 0.5 m/sec. While the wider mouth of the net may have affected the sampling
138 efficiency, the similar mesh size makes the datasets partially comparable. During the two
139 historical cruises, 1946 and 1948, zooplankton were sampled with a closing 168- μ m Juday
140 net (mouth diameter 37 cm), in a manner identical to ours. The species lists produced for
141 the two historical datasets are very detailed for some groups (i.e. copepods), with
142 identification done to species and stage level, but very coarse for others, with just the broad
143 taxonomic categories (i.e. cnidarians, amphipods) listed. The taxonomy during all years
144 was cross-checked using the Arctic Register of Marine species (Sirenko et al. 2019), and
145 World Register of Marine Species (WORMS Editorial Board, 2019) in order to remove
146 synonyms and suspicious identifications. For comparing years, taxonomic assignments
147 within each dataset were adjusted to the highest common denominator. Abundance data
148 from 1946 and 1948 was converted to biomass by using average dry weights for each taxa
149 based on our own results.

150

151 *Data analysis*

152 All analyses were carried out in R (R Core Computing Team 2017). Differences in biomass
153 and abundance of key groups were compared between transects (2015) and years using a
154 one-way ANOVA, with values log-transformed to meet ANOVA assumptions. Within the

155 2015 data, only the top 50 m were included in the analysis to exclude depth-based
156 differences. Zooplankton community structure was investigated using cluster analysis and
157 non-metric multidimensional scaling (nMDS) using the R package “vegan” (Oksanen 2013).
158 Species matrices containing abundance and biomass data were fourth-root transformed;
159 rare groups, which failed to contribute at least 5% to at least one stations were excluded.
160 Key copepod species (*Calanus* spp., *Metridia longa*) were separated by developmental stage
161 into “early juveniles” (CI-CIII) and “late juveniles/adults” (CIV-CVI) as separate categories.
162 Hierarchical cluster analysis was carried out using average linkage; significant clusters
163 were identified using the SIMPROF routine ($\alpha = 0.05$) (Clarke and Gorley, 2005). The
164 resulting clusters were confirmed by separation on a 2-dimensional nMDS ordination. The
165 taxa responsible for discriminating the groups were identified by correlating species
166 abundances to the ordination via the *envfit* function, as well as by the function *IndVal*
167 (Duf rene and Legendre 1997), which finds “indicator” species that are significantly
168 associated with specific groups based on the relative frequency and relative average
169 abundance within each cluster. The relationship of community structure to the
170 environment was explored by correlating environmental parameters to the nMDS
171 ordination using the *envfit* function, with significance established via a permutation test (n
172 = 10000). Additionally, the best set of physical parameters that describes community
173 structure was identified via the BIOENV routine (Clarke and Ainsworth 1993), which
174 selects the set of variables that produce the highest correlation between two data matrices.
175 Significance of these correlations was established using a permutation test ($n = 10000$) at p
176 < 0.05.

177 Zooplankton community structure was also examined within the context of the
178 historical data, similar to the process above, with all sampling years pooled. Only
179 abundance data was used; questionable taxa, or taxa which were not
180 enumerated/identified during all of the expeditions were excluded from analysis. Depth
181 integrated data was used for 2015. The resulting clusters were overlain on an MDS
182 ordination and spatial map of the sampling locations. Taxa responsible for community
183 separation were similarly identified using the *envfit* function.

184

185 **Results**

186 *Oceanographic conditions during September 2015*

187 Sea ice conditions varied from completely open water to 45-60% ice cover at the
188 deeper stations of each transect (Fig. 2). The water column was well stratified along both
189 transects (Fig. 2) with distribution of water masses typical for the Arctic Ocean (Rudels
190 2008 water mass T-S characteristics defined therein). The Polar mixed layer (PML)
191 characterized by a low salinity (<29) and temperature ranging from -1 to 0 °C occupied the
192 top ~20 m. This layer was underlain by the Arctic Halocline, with a higher salinity (>32.5)
193 and colder temperature generally below 0°C. Warm and salty Atlantic Water (AW) (T > 0
194 °C) was found below depths >250 m at the basin stations, and as shallow as 150m at
195 stations along the slope, indicating possible upwelling of AW onto the shelf. A local oxygen
196 minimum, as well as a sharp salinity gradient was observed within the halocline,
197 particularly on Transect 1, possibly indicating two sources of halocline water (with upper
198 halocline of Pacific origin, $32.5 < S < 33.5$ and lower halocline with $33.5 < S < 34.5$, Shimada
199 et al. 2005; Rudels 2008) . Chl-*a* concentrations were low throughout the entire sampled
200 area being highest on the shelf on Transect 1 and reaching up to $2 \mu\text{g L}^{-1}$. Within the surface
201 mixed layer they rarely exceeded $0.2\text{-}0.4 \mu\text{g L}^{-1}$. The chlorophyll maximum was found
202 around ~50m in the basin and near bottom at the shallow shelf stations (Fig. 2).

203

204 *Cross shelf-structure of zooplankton communities*

205 A total of 70 taxonomic categories were identified within the mesozooplankton (Table
206 2), including 41 crustacean species (35 species of copepods, 5 amphipods, 1 ostracod), 14
207 cnidarian species (12 hydromedusae, 1 scyphomedusae, 1 siphonophora), 2 ctenophores, 2
208 pteropods, 2 larvaceans, 3 chaetognaths, and 7 meroplankton taxa (Table 2). However, the
209 number of species at each station and each sampled depth stratum was low, usually not
210 exceeding 20-30 taxa. Diversity increased with depth and away from the shelf margin, with
211 the highest species number observed within the deepest layers at the offshore stations (Fig.
212 3a). Most of the recorded taxa belonged to typical Arctic neritic and Arctic epi- and
213 mesopelagic species, but the species list also included Atlantic (*Calanus finmarchicus*) and
214 Pacific (*Metridia pacifica*, *Eucalanus bungei*) expatriates. Other than *Eurytemora herdmani*,
215 which was observed at one shallowest station, no euryhaline or brackish-water species,

216 characteristic for the shallow river-influenced Siberian shelf seas (Kosobokova et al., 1998;
217 Lischka et al, 2001; Hirche et al, 2006) were observed.

218 The highest abundance of zooplankton was also found at stations along the slope and
219 was concentrated in the surface layer (Fig. 3b); the highest abundances on Transect 1
220 coincided with the highest surface temperatures (Fig. 2a). Abundance was significantly
221 higher in the surface waters (above 65m depth) of Transect 1 than on Transect 2 (ANOVA,
222 $F_{1,14} = 8.93, p = 0.009$). Differences between deeper layers (below 65m) were insignificant.
223 Small copepods *Pseudocalanus* spp. and *Oithona similis* dominated the abundance at all but
224 the farthest offshore stations. Appendicularians *Fritillaria borealis* and *Oikopleura*
225 *vanhoeffeni* were the second most significant contributors to abundance, particularly at the
226 shelf stations (Fig. 4).

227 Zooplankton biomass ranged from 10 to 100 mg DW m⁻³, and was highest at stations at
228 the shelf break on both transects, at depths of 150-250 m (Fig. 3c), mainly driven by the
229 large copepods *Calanus glacialis*, *C. hyperboreus* and *Metridia longa*. At the shallow shelf
230 stations, biomass was lower, not exceeding 10-20 mg DW m⁻³, with *Pseudocalanus* spp.
231 being the main contributors. Chaetognaths represented the next largest contributor to
232 biomass, composing 20-30% of total biomass at all stations. *Parasagitta elegans* dominated
233 on the shelf and slope and *Eukhronia hamata* largely replaced it at the deeper sampling
234 locations (Fig. 4).

235 Multivariate analysis separated zooplankton communities by depth and distance from
236 shore according to both abundance (Fig. 5) and biomass data (Online Resource 1), with
237 surface shelf communities being distinct from surface slope communities, as well as deeper
238 communities at the shelf break. Based on abundance, the community was homogenous in
239 the surface and subsurface layers (0-25 and 25-65 m) at the Transect 1 stations; on
240 Transect 2, on contrary, most stations contained distinct communities in these two layers
241 (Fig 5; Online Resource 1). Based on both the IndVal analysis (Online Resource 2) and
242 correlations to the nMDS ordination (only significant correlations shown), the separation of
243 the **surface shelf communities** was driven by the increased abundance and biomass of the
244 hydromedusae *Calyropsis birulai*, *Aeginopsis laurentii*, the copepods *Microsetella norvegica*,
245 *Acartia longiremis*, as well as adult females of *Calanus glacialis*, and the larvacean
246 *Oikopleura vanhoeffeni*. The **off-shelf surface communities**, mainly observed on the slope,

247 were distinguished by high numbers of the juvenile *Pseudocalanus* spp., juvenile *C. glacialis*
248 and meroplankton: echinoderm, bivalve and polychaete larvae. A few stations on in the
249 surface waters on Transect 2 also clustered as a separate community type, driven by the
250 high abundance of juvenile *Aglantha digitale*, *Fritellaria borealis* and *Oithona similis*. The
251 **sub-surface communities** along the slope were distinguished by the mesopelagic *Triconia*
252 *borealis*, *Metridia longa* (adults and older juveniles), *P. minutus* (adults and older juveniles),
253 *Microcalanus pygmaeus*, *Paraeuchaeta glacialis*, as well as the Pacific expatriates *Eucalanus*
254 *bungii* and *Metridia pacifica*. These stations also contained high biomass of the chaetognath
255 *Parasagitta elegans*. Finally, the **deep communities** in the waters at the shelf break were
256 distinguished by a number of Arctic Basin species, as well as the Atlantic expatriate *Calanus*
257 *finmarchicus*. Biomass data separated the 25-65 m layer as a distinct group only at the
258 slope stations of both transects (Online Resource 1).

259 The MDS ordination was largely determined by sampled depth strata, which distributed
260 stations along Axis 1. It was also strongly and significantly ($p < 0.01$) correlated with
261 physical factors, with salinity and bottom depth having the highest correlations to the
262 ordination (Fig. 5). Chl-*a* concentration, sea ice concentration and temperature were also
263 significantly correlated to the ordination, but explained less of the variability. There was no
264 correlation to distance from ice edge or oxygen concentration. The BIOENV routine
265 predicted layer depth as the most significant factor correlated with community structure (ρ
266 = 0.64), while the inclusion of salinity and bottom depth increased Spearman's correlation
267 to $\rho = 0.7$.

268

269 *Comparison with other datasets*

270 Overall mean abundance and biomass values were similar between years (Table 3),
271 although some significant differences between sampling years were observed in overall
272 zooplankton abundance (ANOVA, $F_{3,44} = 5.71$, $p = 0.00216$) and biomass (ANOVA, $F_{3,44} =$
273 5.94 , $p = 0.00345$), as well as abundance of *Calanus glacialis* (ANOVA, $F_{3,44} = 9.51$, $p <$
274 0.0001). Abundance and biomass were significantly higher in 2009 than during the other
275 sampling years; abundance of *C. glacialis* was significantly higher in 2009 and 2015 than in
276 the two early years (Table 3, Fig. 6). The diversity in 2009 and 2015 was also much higher,
277 due to the absence of Arctic Basin species in the shallow regions explored in 1946 and

278 1948, as well as overall lower taxonomic resolution during the processing of 1946 and
279 1948 samples.

280 Nevertheless, some species were observed during these earlier expeditions that were
281 not recorded (Table 2, Fig. 6). These include the brackish water species *Pseudocalanus*
282 *major* and *Drepanopus bungei*, as well as juvenile and adult euphausiids, which were
283 common in the eastern part of the region during the three expeditions prior to 2015.
284 Multivariate analysis (cluster analysis and MDS) grouped stations from all the four
285 expeditions into 5 groups with two outliers (Fig. 7). The most distinct group was the
286 stations west of Chaun Bay (coral color on Fig. 7), characterized by the dominance of
287 brackish *P. major* and *D. bungei*, which were observed nowhere else, as well as extremely
288 low abundance and biomass of all other species. The stations near Chaun Bay formed a
289 distinct group (green color on Fig. 7), separated by the presence of brackish *P. major* and
290 *Limnocalanus macrurus*. The remainder of the shelf stations belonged to two groups: one
291 common to all expeditions (yellow color on Fig. 7), with the separation driven by the
292 abundance of hydrozoan jellyfish, harpacticoid copepods, appendicularians, and
293 meroplankton. The other group (pink color on Fig. 7) was unique to 2009 and was
294 characterized by the higher abundances of the hydrozoan jellyfish *Aeginopsis laurentii* and
295 the chaetognath *Parasagitta elegans*. All stations deeper than 50 m (all from 2015) grouped
296 together, characterized by typical Arctic Basin communities. Pacific expatriates, with the
297 exception of euphausiids, were generally only observed during the 2015 expedition at
298 stations deeper than the shelf break.

299

300 **Discussion**

301 The patterns of zooplankton abundance and diversity across the shelf as well as
302 through the vertical column in the northern region of the East Siberian Sea during our
303 study in 2015 generally followed those observed earlier in other parts of the Arctic, with
304 highest zooplankton abundance and biomass found in the surface layers, and increasing
305 diversity with depth (Fig. 3) (Kosobokova et al. 1998; Ashjian et al. 2003; Hirche et al.
306 2006; Kosobokova and Hirche 2009). A marked hotspot of both abundance and biomass
307 was observed close to the shelf break, with much lower values observed both farther on-
308 and off- the shelf. The biomass peak at the shelf break was mainly driven by *Calanus*

309 *glacialis*, which similarly concentrated at the outer shelf and slope in other parts of the
310 Arctic, substantially contributing to the “carbon belt” of elevated zooplankton biomass
311 around the entire Eurasian slope (Kosobokova and Hirche 2009; Kosobokova 2012). The
312 vertical structure of zooplankton communities in the northern ESS was fairly typical for
313 other regions of the Arctic, with distinct communities in the surface, sub-surface and
314 mesopelagic layers (Kosobokova and Hopcroft 2010; Kosobokova et al. 2011). The upper
315 limit of the range and mean biomass we observed in the northern ESS (10-100mg DW,
316 mean ~30 mg DW) was higher than previously reported for the ESS, similar to the Laptev
317 and Kara Seas (Kosobokova et al. 1998; Fahl et al. 1999; Abramova and Tuschling 2005;
318 Arashkevich et al. 2018). They were, however, lower than in the adjacent Chukchi Sea
319 (Questel et al. 2013; Ershova et al. 2015b), which experiences a much longer productive
320 period and a high inflow of nutrients and allochthonous biomass from the North Pacific.

321 Semiletov et al. (2005) suggested that oceanographically the East Siberian Sea can
322 be separated into two distinct regions: the river-influenced western region and the Pacific-
323 influenced eastern region, separated by a frontal zone which position fluctuates year-to-
324 year between 160° and 170° E. While our combined dataset is mostly concentrated west of
325 this front, our data suggests distinct regional differences in zooplankton community
326 structure between these two regions. The inner western stations (all sampled in 1948),
327 heavily influenced by river outflow, are characterized by overall low abundance, diversity,
328 and dominance of brackish species, which were not observed elsewhere. The outer shelf
329 stations (sampled in 2015), although also located far enough to the west, did not capture
330 any of this brackish signature, which is likely a consequence of the river-influenced domain
331 being restricted only to the inner shelf. Alternatively, it is possible that during 2015 the
332 frontal zone separating the two domains was located farther to the west. It is noteworthy
333 that all remaining shelf stations were similar in zooplankton community structure, both in
334 present times and 75 years ago, and contained typical Arctic neritic fauna, which is shared
335 with adjacent Siberian Arctic seas (Kosobokova et al. 1998; Lischka et al. 2001; Hirche et al.
336 2006; Flint et al. 2010). Our data suggest that Long Strait and the area around Wrangel
337 Island may represent yet another community type, possibly influenced by increased flow
338 from the Chukchi Sea (Coachman and Rankin 1968; Pisareva et al. 2015). And, finally, at the
339 shelf break, the zooplankton communities transitioned to typical Arctic Basin type

340 containing a much higher diversity compared to the shallow ESS shelf, and characteristic
341 Arctic Basin type of vertical structure (Kosobokova and Hopcroft 2010; Kosobokova et al.
342 2011).

343 As an interior arctic shelf sea (Williams and Carmack 2015), the ESS has limited
344 exchange with other oceans as well as adjacent regions of the Arctic when compared to
345 regions of inflow/outflow (the Barents Sea, Chukchi Sea), but advection still plays an
346 important role in structuring its pelagic communities. It is noteworthy that the ESS is one of
347 the few locations in the Arctic influenced by inflow both from the Atlantic and Pacific
348 oceans. One striking result of our study in this context is the record of both Atlantic and
349 Pacific expatriates (the copepods *Calanus finmarchicus*, *Eucalanus bungii*, *Metridia pacifica*)
350 in our study area in 2015, albeit in fairly low numbers, and the Pacific expatriates
351 euphausiids *Thysanoessa* spp. in 1946, 1948 and 2009 (although we cannot exclude that
352 they represent a local reproducing population). The advected copepods were generally
353 found in the water layers below 50m, and all observed specimens were adults/sub-adults,
354 indicating that they probably have been in transit for an extended period. A period of 5-6
355 years is required for inflowing Atlantic water to reach the East Siberian Sea, (E. Carmack,
356 pers. comm.). Although lifespans of pelagic copepods have never been measured in natural
357 conditions, it is generally believed that few are capable of surviving for 5+ years (Hirche
358 2013). Tracking the advected organisms could be a useful tool in determining the
359 pathways, extent and transit time of Atlantic and Pacific water entering the Arctic.

360 While both shelf and off-shelf regions of the ESS may be influenced by Pacific water
361 (Semiletov et al. 2005), the taxonomic composition of Pacific expatriates is very different in
362 the two regions. On the inner shelf, euphausiids *Thysanoessa* spp., which are also not
363 presumed to reproduce in the Arctic and are not found farther to the west, were observed
364 during nearly every sampling year (1947, 1948, 2009), but Pacific copepods were absent or
365 overlooked. At the off-shelf stations, the reverse was true, with the Pacific copepods
366 *Eucalanus bungii* and *Metridia pacifica* being prominent members of the communities
367 (2015). This is suggestive of two distinct sources of Pacific water present in the region: the
368 more “short-term” water entering the ESS through Long Strait from the Chukchi Sea
369 (Semiletov et al. 2005), containing entrapped euphausiids, and the “older” Pacific water,
370 which has been in transit for at least one season (Bluhm et al., 2015), entering from the

371 Canadian Basin away from the shelf. It is unclear why we also do not observe Pacific
372 copepods in the Long Strait region. As they are oceanic species, originating on the Bering
373 Sea slope by the Gulf of Anadyr, perhaps they cannot survive the low salinity conditions of
374 this region, which is influenced by the fresh waters of the Siberian Coastal Current
375 (Weingartner et al. 1999). It is also quite possible that part of the *C. glacialis* that we
376 observe in the area belongs to the north Bering Sea population that is advected through the
377 Bering Strait (Nelson et al. 2009). The latter point is impossible to clarify without genetic
378 studies.

379 Historically, the ESS has been one of the most heavily ice covered regions of the
380 Arctic (Nghiem et al. 2006), but has in recent decades transitioned into part of the seasonal
381 ice zone, with extended areas of open water during the summer months (Maslanik et al.
382 2007). The decline in sea ice extent and duration, as well as increasing Atlantification
383 (Polyakov et al. 2017) of the Eastern Arctic are shifting the conditions in to resemble those
384 in the western Eurasian Basin, and such a shift is expected to be reflected in the structure
385 and/or productivity of biological communities. Although the data we collected is
386 insufficient to document change, the significantly higher abundance of zooplankton,
387 particularly *Calanus glacialis*, that we observed during recent years (2009, 2015), may
388 suggest that this Atlantification is already having an effect on the region. Of course, such
389 conclusions must be reached with caution, given the different spatial coverage and
390 sampling methods during the different expeditions. However, these changes would not be
391 entirely surprising, given the trends of increasing of zooplankton advection into the Arctic
392 (Johannesen et al. 2012; Gluchowska et al. 2017), including the adjacent Chukchi Sea
393 (Ershova et al. 2015a). We expect our study to provide the important information on the
394 present state of the plankton communities of this understudied arctic sea and will serve as
395 a valuable baseline to document further change within this region.

396

397 **Acknowledgements**

398 The shipboard collections of zooplankton were conducted within the NABOS program, and
399 the authors acknowledge Igor Polyakov, Vladimir Ivanov, Vladimir Gagarin, Dmitry Kulagin,
400 as well as the crew and scientists of RV “Professor Tryoshnikov”. The work of EE has
401 been jointly funded by UiT the Arctic university of Norway and the Tromsø Research

402 Foundation under the project "Arctic Seasonal Ice Zone Ecology", project number
403 01vm/h15. We thank Elena Markhaseva and Russell Hopcroft for providing additional data
404 from previous expeditions. Data processing and manuscript preparation was supported by
405 the Russian Ministry of Science and Education, agreement number 298 14.616.21.0078
406 (RFMEFI61617X0078). We thank the three anonymous reviewers who improved the
407 manuscript with their comments.

408

409 **References**

- 410 Abramova E, Tuschling K (2005) A 12-year study of the seasonal and interannual dynamics
411 of mesozooplankton in the Laptev Sea: Significance of salinity regime and life cycle
412 patterns. *Glob Planet Change* 48:141–164. doi: 10.1016/j.gloplacha.2004.12.010
- 413 Anderson LG, Björk G, Jutterström S, et al (2011) East Siberian Sea, an Arctic region of very
414 high biogeochemical activity. *Biogeosciences* 8:1745–1754. doi: 10.5194/bg-8-1745-
415 2011
- 416 Arashkevich EG, Drits AV, Pasternak AF, et al (2018) Distribution and feeding of
417 herbivorous zooplankton in the Laptev Sea. *Oceanology* 58:381–395. doi:
418 10.1134/S0001437018030013
- 419 Ashjian CJ, Campbell RG, Welch HE, et al (2003) Annual cycle in abundance, distribution,
420 and size in relation to hydrography of important copepod species in the western Arctic
421 Ocean. *Deep Res Part I Oceanogr Res Pap* 50:1235–1261. doi: 10.1016/S0967-
422 0637(03)00129-8
- 423 Brodsky KA (1957) The copepod fauna (Calanoida) and zoogeographic zonation of the
424 North Pacific and adjacent waters. *Izvestiya Akademii Nauk SSSR, Leningrad*
- 425 Buchholz F, Werner T, Buchholz C (2012) First observation of krill spawning in the high
426 Arctic Kongsfjorden, west Spitsbergen. *Polar Biol* 35:1273–1279. doi:
427 10.1007/s00300-012-1186-3
- 428 Cavalieri D, Parkinson C, Gloersen P, Zwally HJ (1996) Sea ice concentrations from Nimbus-
429 7 SMMR and DMSP SSM/I passive microwave data, Version 1. Years 2010-2015.
430 Boulder, Color. USA. NASA Natl. Snow Ice Data Cent. Distrib. Act. Arch. Center. 2010–
431 2015
- 432 Clarke KR, Ainsworth M (1993) A method of linking multivariate community structure to

433 environmental variables. *Mar Ecol Prog Ser* 92:205–219. doi: 10.3354/meps092205
434 Coachman LK, Rankin DA (1968) Currents in Long Strait, Arctic Ocean Long Strait, Arctic
435 Ocean. *Source Arct* 21:27–38. doi: 10.2307/40507483
436 Dobrovolskii AD, Zalogin BS (1982) *The Seas of the USSR*. Moscow State University,
437 Moscow
438 Dufrêne M, Legendre P (1997) Species assemblages and indicator species: The need for a
439 flexible asymmetrical approach. *Ecol Monogr* 67:345–366. doi: 10.2307/2963459
440 Ershova EA, Hopcroft RR, Kosobokova KN, et al (2015a) Long-Term Changes in Summer
441 Zooplankton Communities of the Western Chukchi Sea, 1945–2012. *Oceanography*
442 28:100–115. doi: 10.5670/oceanog.2015.60
443 Ershova EA, Hopcroft RR, Kosobokova KN (2015b) Inter-annual variability of summer
444 mesozooplankton communities of the western Chukchi Sea: 2004–2012. *Polar Biol*
445 38:1461–1481. doi: 10.1007/s00300-015-1709-9
446 Fahl K, Cremer H, Erlenkeuser H, et al (1999) Sources and pathways of organic carbon in
447 the modern Laptev Sea (Arctic Ocean): Implications from biological, geochemical and
448 geological data. *Polarforschung* 69:193–205
449 Flint MV, Semenova TN, Arashkevich EG, et al (2010) Structure of the zooplankton
450 communities in the region of the Ob River’s estuarine frontal zone. *Oceanology*
451 50:766–779. doi: 10.3324/haematol.2015.132142
452 Gluchowska M, Dalpadado P, Beszczynska-Möller A, et al (2017) Interannual zooplankton
453 variability in the main pathways of the Atlantic water flow into the Arctic Ocean (Fram
454 Strait and Barents Sea branches). *ICES J Mar Sci* 74:1921–1936. doi:
455 10.1093/icesjms/fsx033
456 Grebmeier JM, Maslowski W (2014) *The Pacific Arctic Region: Ecosystem status and trends*
457 *in a rapidly changing environment*. Springer, Berlin-Heidelberg-New York
458 Hirche HJ (2013) Long-term experiments on lifespan, reproductive activity and timing of
459 reproduction in the Arctic copepod *Calanus hyperboreus*. *Mar Biol* 160:2469–2481.
460 doi: 10.1007/s00227-013-2242-4
461 Hirche HJ, Kosobokova KN, Gaye-Haake B, et al (2006) Structure and function of
462 contemporary food webs on Arctic shelves: A panarctic comparison. The pelagic
463 system of the Kara Sea - Communities and components of carbon flow. *Prog Oceanogr*

464 71:288–313. doi: 10.1016/j.pocean.2006.09.010

465 Johannesen E, Ingvaldsen RB, Bogstad B, et al (2012) Changes in Barents Sea ecosystem
466 state, 1970–2009: Climate fluctuations, human impact, and trophic interactions. *ICES J*
467 *Mar Sci* 69:880–889. doi: 10.1093/icesjms/fss046

468 Kassens H, Bauch HA, Dmitrenko IA, et al (1999) *Land-Ocean Systems in the Siberian*
469 *Arctic: Dynamics and History*. Springer-Verlag, Berlin-Heidelberg-New York

470 Kosobokova KN (2012) *Zooplankton of the Arctic Ocean: Community structure, ecology,*
471 *spatial distribution*. GEOS, Moscow

472 Kosobokova KN, Hanssen H, Hirche HJ, Knickmeier K (1998) Composition and distribution
473 of zooplankton in the Laptev Sea and adjacent Nansen Basin during summer, 1993.
474 *Polar Biol* 19:63–76. doi: 10.1007/s003000050216

475 Kosobokova KN, Hirche HJ (2009) Biomass of zooplankton in the eastern Arctic Ocean - A
476 base line study. *Prog Oceanogr* 82:265–280. doi: 10.1016/j.pocean.2009.07.006

477 Kosobokova KN, Hopcroft RR (2010) Diversity and vertical distribution of
478 mesozooplankton in the Arctic's Canada Basin. *Deep Sea Res Part II Top Stud Oceanogr*
479 57:96–110. doi: 10.1016/j.dsr2.2009.08.009

480 Kosobokova KN, Hopcroft RR, Hirche HJ (2011) Patterns of zooplankton diversity through
481 the depths of the Arctic's central basins. *Mar Biodivers* 41:29–50. doi:
482 10.1007/s12526-010-0057-9

483 Kwok R, Cunningham GF, Wensnahan M, et al (2009) Thinning and volume loss of the
484 Arctic Ocean sea ice cover: 2003–2008. *J Geophys Res Ocean* 114. doi:
485 10.1029/2009JC005312

486 Lischka S, Knickmeier K, Hagen W (2001) Mesozooplankton assemblages in the shallow
487 Arctic Laptev Sea in summer 1993 and autumn 1995. *Polar Biol* 24:186–199. doi:
488 10.1007/s0030000000195

489 Markhaseva EL, Golikov AA, Agapova TA, et al (2005) *Archives of the Arctic Seas*
490 *Zooplankton*. In: *Contributions from the Zoological Institute*. Russian Academy of
491 *Sciences*, St. Petersburg

492 Maslanik JA, Fowler C, Stroeve J, et al (2007) A younger, thinner Arctic ice cover: Increased
493 potential for rapid, extensive sea-ice loss. *Geophys Res Lett* 34. doi:
494 10.1029/2007GL032043

495 Münchow A, Weingartner TJ, Cooper LW (1999) The Summer Hydrography and Surface
496 Circulation of the East Siberian Shelf Sea. *J Phys Oceanogr* 29:2167–2182. doi:
497 10.1175/1520-0485(1999)029<2167:TSHASC>2.0.CO;2

498 Nelson RJ, Carmack EC, McLaughlin FA, Cooper GA (2009) Penetration of pacific
499 zooplankton into the western arctic ocean tracked with molecular population genetics.
500 *Mar Ecol Prog Ser* 381:129–138. doi: 10.3354/meps07940

501 Nghiem S V., Chao Y, Neumann G, et al (2006) Depletion of perennial sea ice in the East
502 Arctic Ocean. *Geophys Res Lett* 33. doi: 10.1029/2006GL027198

503 Oksanen J (2013) *Multivariate Analysis of Ecological Communities in R*. R Top. Doc.

504 Pavshchikov EA (1994) An overview of the composition and quantitative distribution of
505 zooplankton in the East-Siberian Sea. *Issled Fauny Morey* 48:17–46

506 Pinchuk AI (1994) On zooplankton of Chaun Bay. In: *Ecosystems, flora and fauna of Chaun*
507 *Bay, East-Siberian Sea*, 47(55). *Issledovaniya Fauny Morey*, Saint Petersburg, pp 121–
508 127

509 Pipko II, Semiletov IP, Pugach SP, et al (2011) Interannual variability of air-sea CO₂ fluxes
510 and carbon system in the East Siberian Sea. *Biogeosciences* 8:1987–2007. doi:
511 10.5194/bg-8-1987-2011

512 Pisareva MN, Pickart RS, Spall MA, et al (2015) Flow of Pacific water in the western Chukchi
513 Sea: Results from the 2009 RUSALCA expedition. *Deep Res Part I Oceanogr Res Pap*
514 105:53–73. doi: 10.1016/j.dsr.2015.08.011

515 Polyakov I V., Pnyushkov A V., Alkire MB, et al (2017) Greater role for Atlantic inflows on
516 sea-ice loss in the Eurasian Basin of the Arctic Ocean. *Science* 356:285–291. doi:
517 10.1126/science.aai8204

518 Questel JM, Clarke C, Hopcroft RR (2013) Seasonal and interannual variation in the
519 planktonic communities of the northeastern Chukchi Sea during the summer and early
520 fall. *Cont Shelf Res* 67:23–41. doi: 10.1016/j.csr.2012.11.003

521 R Core Computing Team (2017) *R: A Language and Environment for Statistical Computing*.
522 *R Found Stat Comput*. doi: ISBN 3-900051-07-0

523 Roff JC, Hopcroft RR (1986) High precision microcomputer based measuring system for
524 ecological research. *Can J Fish Aquat Sci* 43:2044–2048. doi: 10.1139/f86-251

525 Rudels B (2008) Arctic Ocean Circulation. In: Steele JH, Thorpe S, Turekian K (eds)

526 Encyclopedia of Ocean Sciences, 2nd edn. Elsevier, pp 211–225
527 Semiletov I, Dudarev O, Luchin V, et al (2005) The East Siberian Sea as a transition zone
528 between Pacific-derived waters and Arctic shelf waters. *Geophys Res Lett* 32. doi:
529 10.1029/2005GL022490
530 Shimada K, Itoh M, Nishino S, et al (2005) Halocline structure in the Canada Basin of the
531 Arctic Ocean. *Geophys Res Lett* 32 doi: 10.1029/2004GL021358
532 Sirenko BI, Clarke C, Hopcroft RR, et al (2019) The Arctic Register of Marine Species
533 (ARMS) compiled by the Arctic Ocean Diversity (ArcOD) project.
534 <http://www.marinespecies.org/arms>
535 Stein R, Fahl K, Fütterer D, et al (eds) (2004) *Siberian river run-off in the Kara Sea*. Elsevier,
536 Amsterdam
537 Vihtakari M, Welcker J, Moe B, et al (2018) Black-legged kittiwakes as messengers of
538 Atlantification in the Arctic. *Sci Rep* 8. doi: 10.1038/s41598-017-19118-8
539 Weingartner TJ, Danielson S, Sasaki Y, et al (1999) The Siberian Coastal Current: A wind-
540 and buoyancy-forced Arctic coastal current. *J Geophys Res Ocean* 104:29697–29713.
541 doi: 10.1029/1999JC900161
542 Williams WJ, Carmack EC (2015) The “interior” shelves of the Arctic Ocean: Physical
543 oceanographic setting, climatology and effects of sea-ice retreat on cross-shelf
544 exchange. *Prog Oceanogr* 139:24–41. doi: 10.1016/j.pocean.2015.07.008
545 WORMS Editorial Board (2019) *World Register of Marine Species*.
546 <http://www.marinespecies.org>

547

548

549 **Figures**

550

551 **Figure 1** Sampling locations in the East Siberian Sea during September 2015 and sampling
552 locations of other expeditions included in the dataset (1946, 1948 and 2009)

553 **Figure 2** Sea ice concentration, salinity, temperature, oxygen and Chl-*a* distributions along
554 Transect 1 (a) and Transect 2 (b). Dashed lines delineate presumed water masses

555 **Figure 3** Depth-stratified distribution of abundance (ind m⁻³), biomass (mg DW m⁻³), and
556 diversity (number of species) along Transects 1 and 2 in the East-Siberian Sea

557 **Figure 4** Relative contribution of most common species to (a) biomass and (b) abundance
558 in September 2015 across Transect 1 in the East Siberian Sea (Transect 2 followed similar
559 trends where the depth ranges overlapped). The diameter of the circles at the top of the
560 columns indicate total abundance/biomass.

561 **Figure 5** (a) results of non-metric multidimensional scaling and cluster analysis of fourth
562 root-transformed zooplankton abundance in the East-Siberian Sea during September 2015
563 and (b) locations of clusters along the sampled transects. Each symbol represents one
564 sample; symbol types represent sampled depth strata; colors indicate significant clusters.
565 Vectors show correlations of species abundances and physical parameters to the
566 ordination (with length reflecting the correlation coefficient r)

567 **Figure 6** Distribution of (a) overall zooplankton abundance, (b) overall zooplankton
568 biomass, and (c-e) select zooplankton species in the East-Siberian Sea during 1946, 1948,
569 2009 and 2015

570 **Figure 7** (a) results of non-metric multidimensional scaling and cluster analysis of fourth
571 root-transformed abundance data for all years pooled, and (b) spatial distribution of
572 clusters. Each symbol represents one sample; symbol types represent sampling year; colors
573 indicate significant clusters. Vectors show correlations of species abundance to the
574 ordination (with length reflecting the correlation coefficient r)

575 **ESM1** (a) results of non-metric multidimensional scaling and cluster analysis of fourth log-
576 transformed zooplankton biomass in the East-Siberian Sea during September 2015 and (b)
577 locations of clusters along the sampled transects. Each symbol represents one sample;
578 symbol types represent sampled depth strata; colors indicate significant clusters. Vectors
579 show correlations of species abundances and physical parameters to the ordination (with
580 length reflecting the correlation coefficient r)

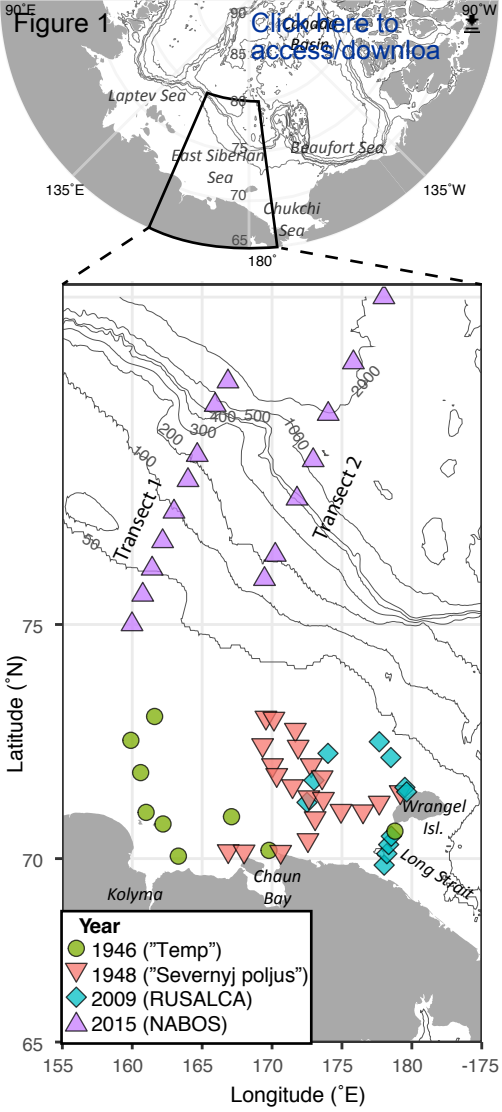
581

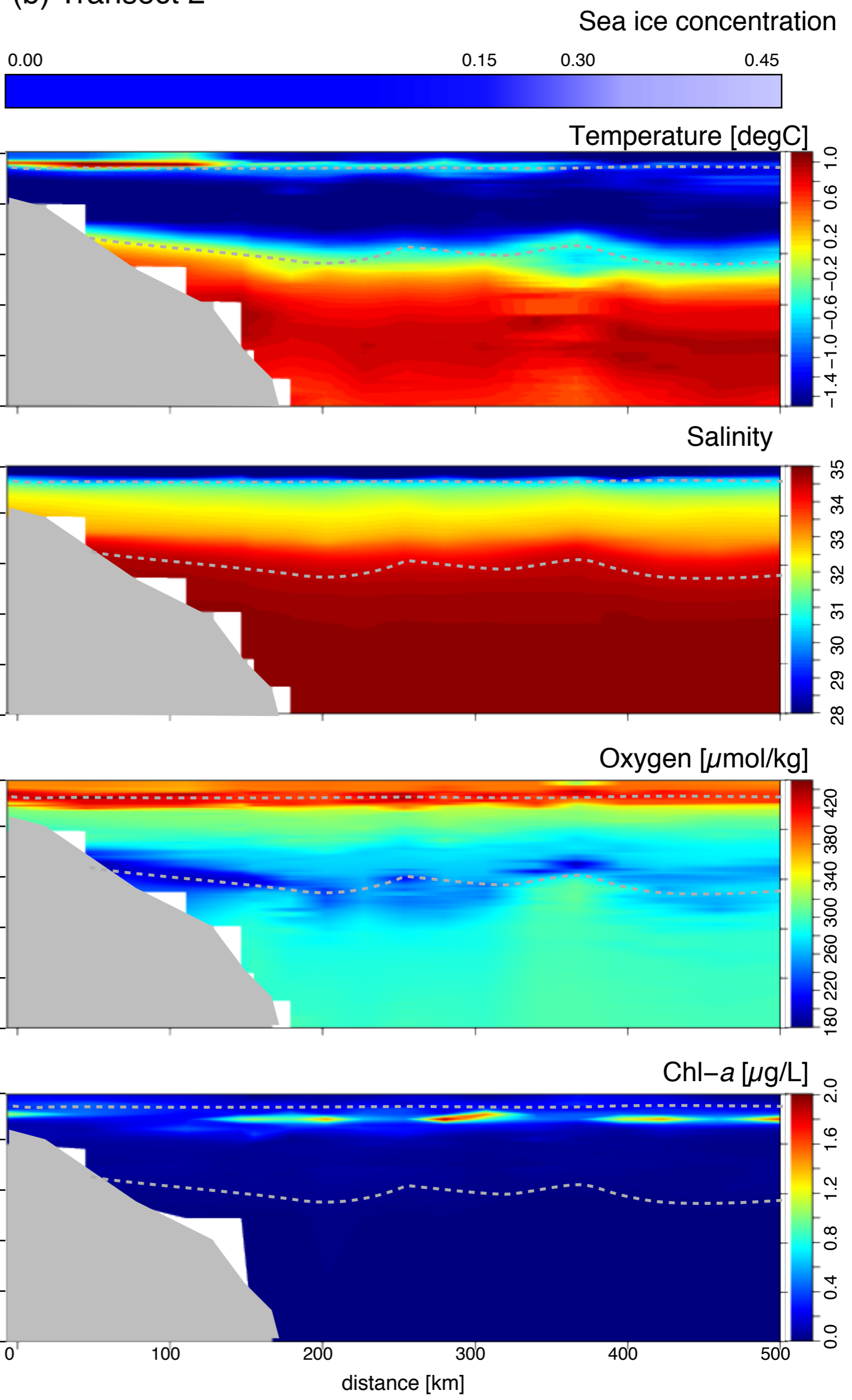
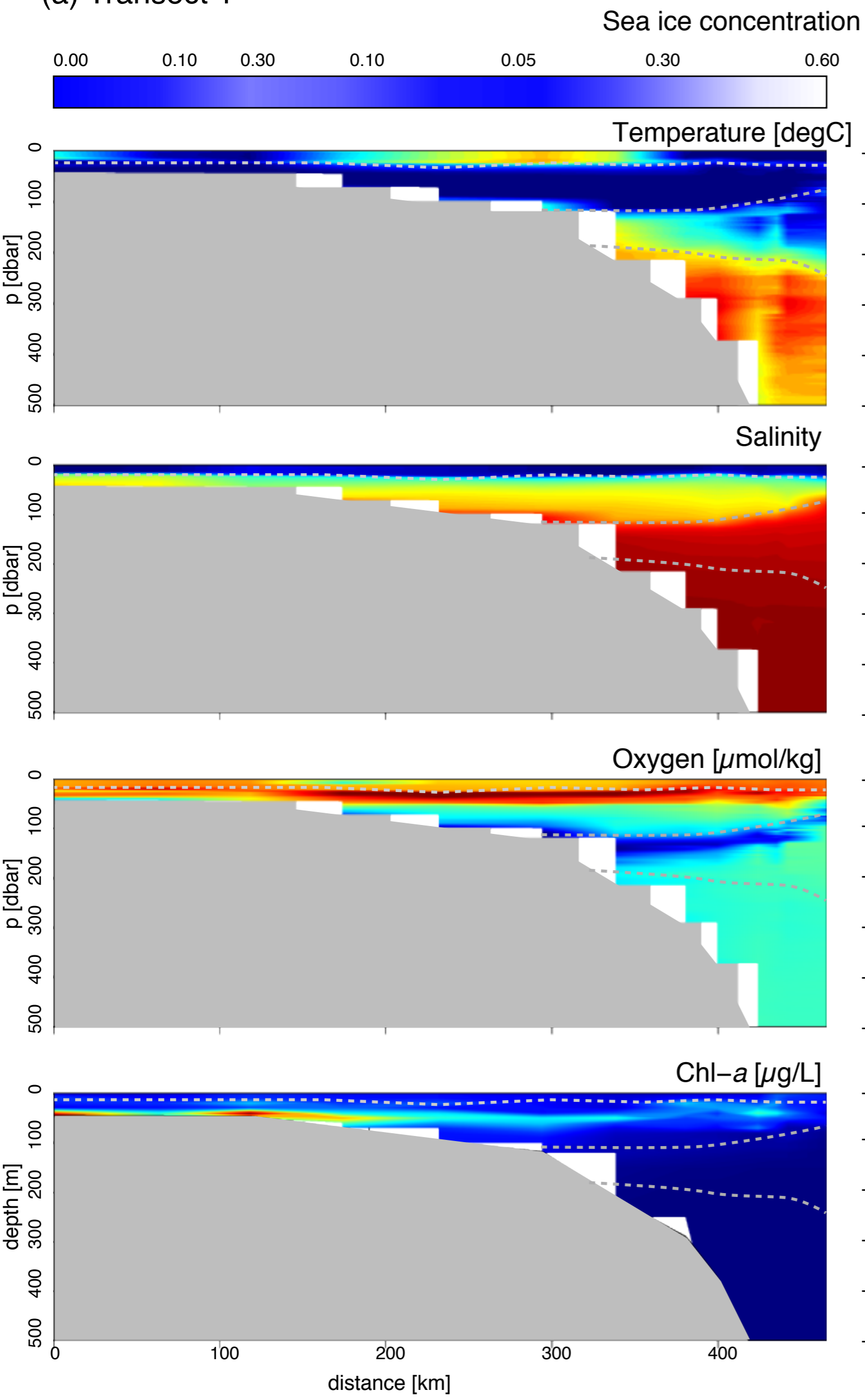
582

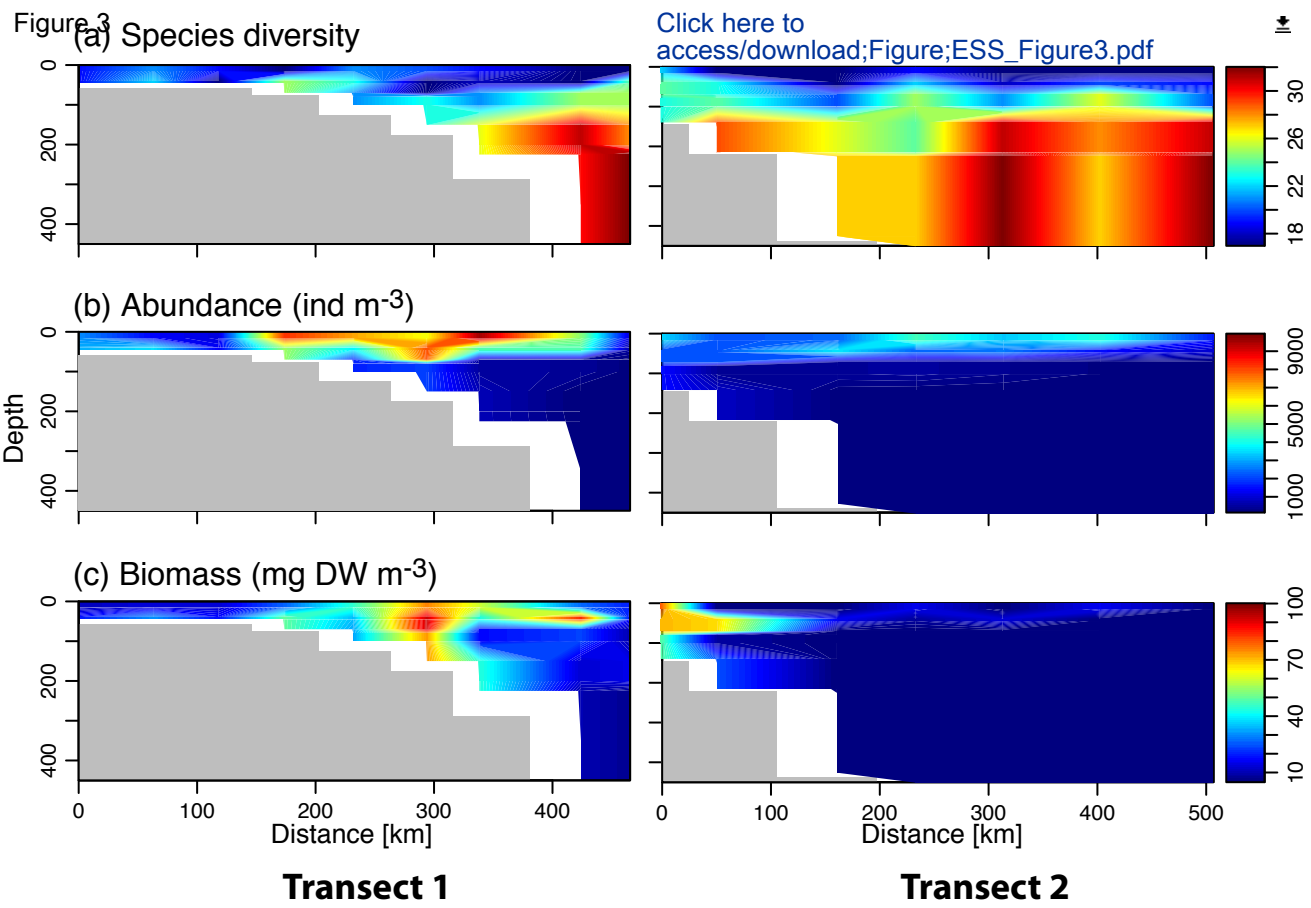
583 **Compliance with Ethical Standards**

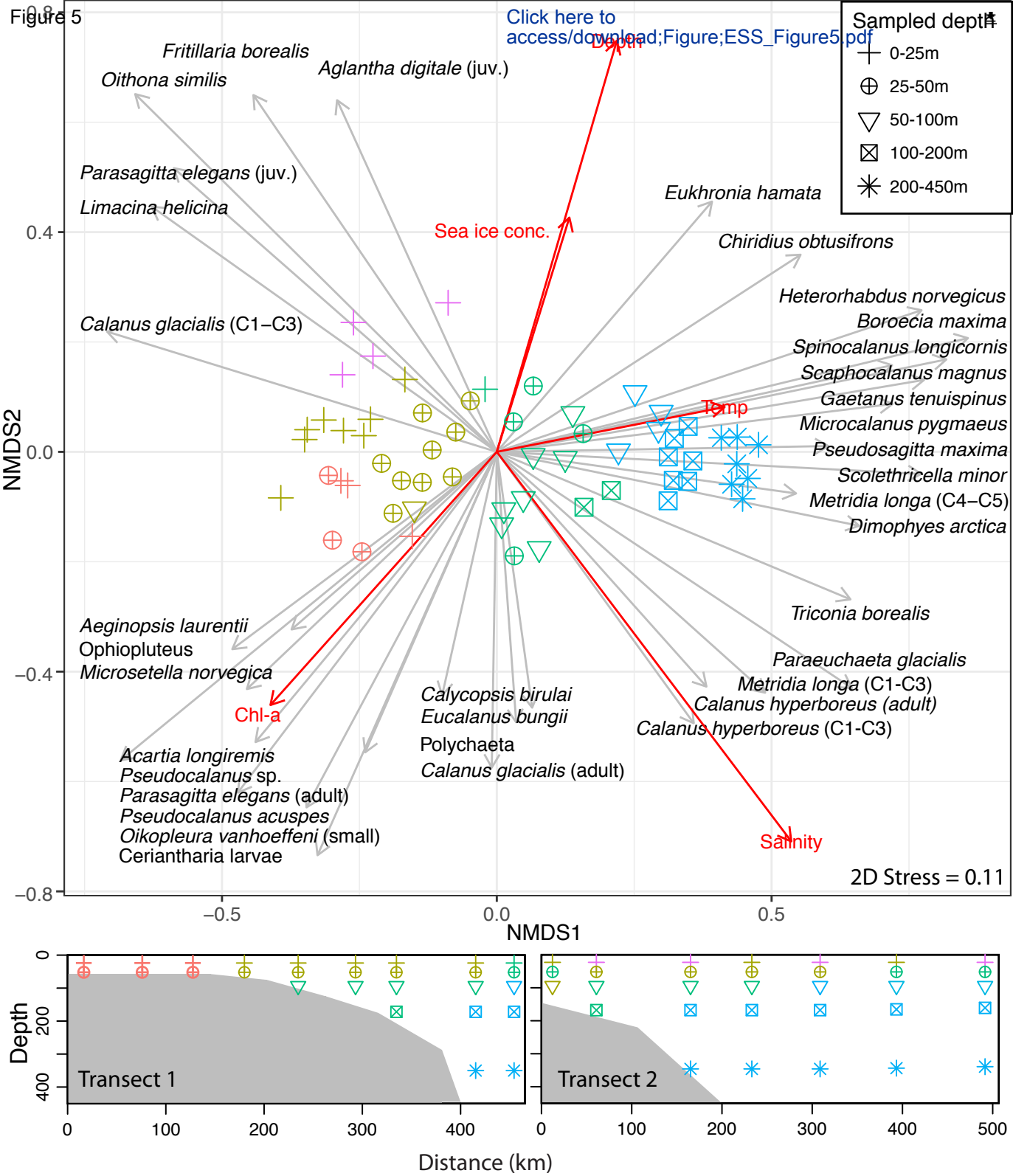
584 *The authors declare that the research was conducted in the absence of any commercial or*
585 *financial relationships that could be construed as a potential conflict of interest.*

586









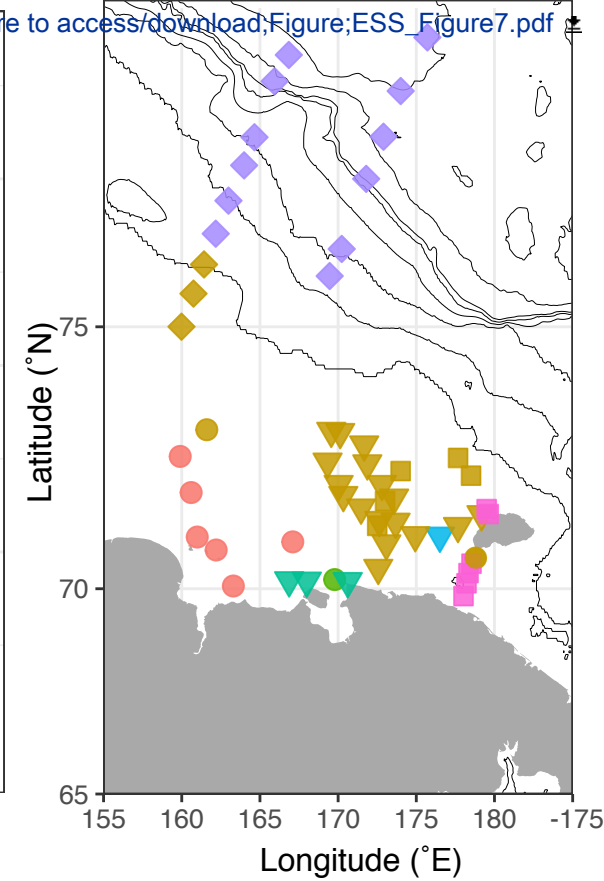
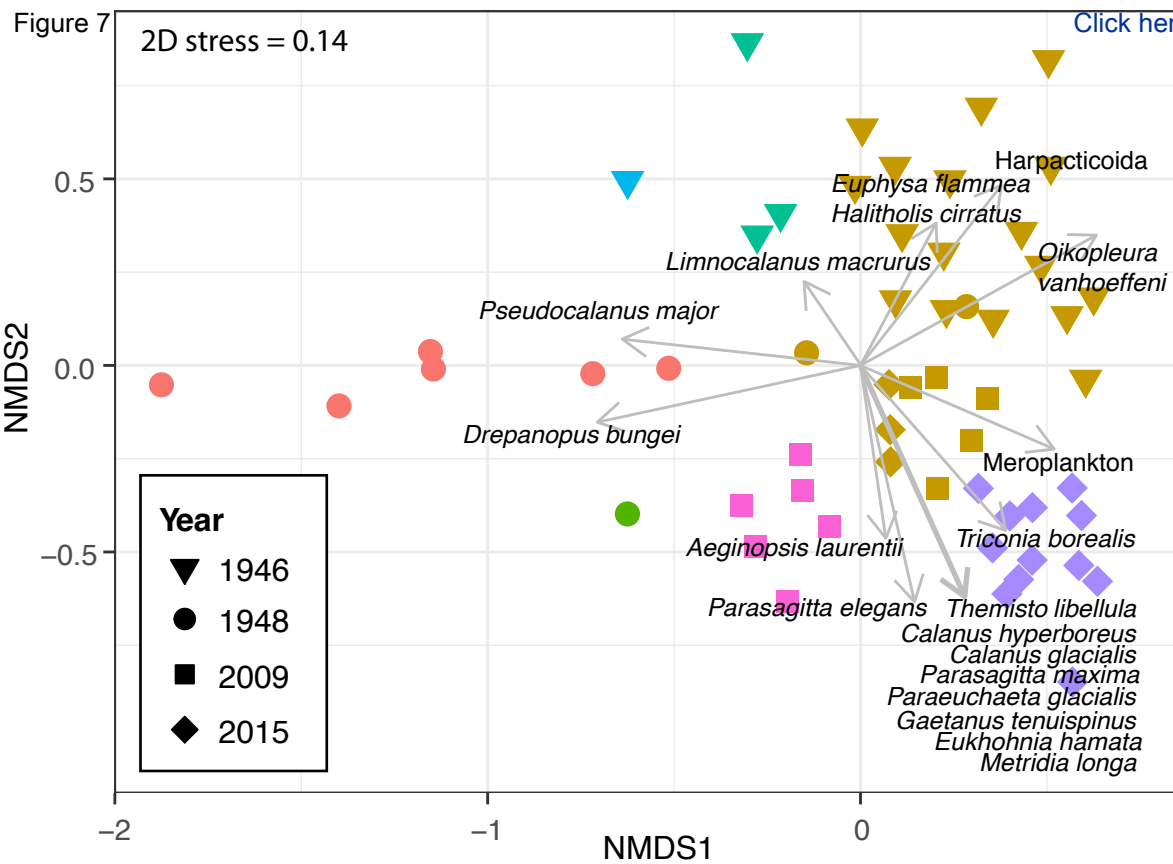


Table 1. Average abundance (ind m⁻³) and biomass (mg DW m⁻³) of all zooplankton species observed during 1946, 1948, 2009, and 2015 in the ESS. “+” – indicates values <0.1; “obs.” – species were observed but not enumerated; “-” – no data.

Species	1946 (data from Markhaseva et al. 2005)		1948 (Pavshits, 1994)		2009 (Ershova et al., 2015a)		2015 (This study)	
	Abund.	Biom.*	Abund.	Biom.*	Abund.	Biom.	Abund.	Biom.
Copepoda								
<i>Acartia longiremis</i>	75.9	0.4	19.8	0.1	36.1	0.1	4.8	+
<i>Aetideopsis rostrata</i>	-	-	-	-	-	-	0.3	+
<i>Bradyidius similis</i>	-	-	-	-	-	-	4.0	0.1
Aetideidae	-	-	-	-	-	-	0.2	+
<i>Calanus finmarchicus</i>	-	-	-	-	-	-	0.6	0.1
<i>Calanus glacialis</i>	17.9	1.5	106.9	16.0	147.3	10.6	75.1	8.8
<i>Calanus hyperboreus</i>	-	-	-	-	0.1	0.3	7.0	3.7
<i>Chiridius obtusifrons</i>	-	-	-	-	-	-	0.8	0.2
<i>Disco triangularis</i>	-	-	-	-	-	-	0.2	0.3
<i>Drepanopus bungei</i>	-	-	871.3	2.2	-	-	-	-
<i>Eucalanus bungii</i>	0.4	0.1	-	-	-	-	0.3	0.1
<i>Eurytemora herdmani</i>	-	-	-	-	-	-	1.1	+
<i>Gaetanus brevispinus</i>	-	-	-	-	-	-	+	+
<i>Gaetanus tenuispinus</i>	-	-	-	-	1.0	0.1	1.2	0.2
<i>Heterorhabdus norvegicus</i>	-	-	-	-	-	-	1.0	0.1
<i>Jaschnovia brevis</i>	-	-	-	-	-	-	10.1	0.2
<i>Jaschnovia tolli</i>	24.7	1.9	31.9	1.0	-	-	0.6	+
<i>Jaschnovia</i> sp.	-	-	-	-	-	-	1.3	+
<i>Limnocalanus macrurus</i>	3.7	+	-	-	-	-	-	-
<i>Metridia longa</i>	-	-	-	-	6.8	0.9	30.3	1.9
<i>Metridia pacifica</i>	-	-	-	-	-	-	1.2	0.2
<i>Microcalanus pygmaeus</i>	67.1	0.1	19.8	+	1.3	+	34.2	0.1
<i>Microsetella norvegica</i>	-	-	-	-	123.1	0.9	4.1	+
<i>Paraeuchaeta glacialis</i>	-	-	-	-	-	-	0.9	0.6
<i>Paraeuchaeta barbata</i>	-	-	-	-	-	-	+	+
<i>Paraeuchaeta polaris</i>	-	-	-	-	-	-	+	+
<i>Paraheterorhabdus compactus</i>	-	-	-	-	-	-	+	+
<i>Pseudocalanus newmani</i>	-	-	-	-	-	-	4.0	+
<i>Pseudocalanus acuspes</i>	-	-	-	-	26.8	0.3	38.6	0.3
<i>Pseudocalanus major</i>	13.8	0.1	119.4	0.3	-	-	-	-
<i>Pseudocalanus minutus</i>	-	-	-	-	3.6	0.1	30.8	0.3
<i>Pseudocalanus</i> sp.	913.7	2.3	285.5	0.7	4331.8	10.3	1140.8	3.4
<i>Scaphocalanus brevicornis</i>	-	-	-	-	-	-	+	+
<i>Scaphocalanus magnus</i>	-	-	-	-	-	-	0.4	0.2
<i>Scolettrichella minor</i>	-	-	-	-	-	-	1.1	+
<i>Spinocalanus antarcticus</i>	-	-	-	-	-	-	+	+
<i>Spinocalanus longicornis</i>	-	-	-	-	-	-	5.6	+
<i>Temorites brevis</i>	-	-	-	-	-	-	+	+
Other calanoida	-	-	-	-	-	-	1.2	0.1

Calanoida nauplii	1170.4	0.1	418.8	0.1	989.7	0.6	189.8	0.3
Harpacticoida	209.5	0.7	17.3	0.1	13.3	0.1	0.4	0.1
<i>Oithona similis</i>	411.9	0.6	225.7	0.3	1836.7	2.7	653.0	0.7
<i>Triconia borealis</i>	60.8	0.1	-	-	0.2	+	37.7	0.1
Cyclopoida	-	-	-	-	-	-	0.5	+
Cnidaria								
<i>Aeginopsis laurentii</i>	2.5	0.1	2.6	0.1	8.2	0.2	3.9	0.1
<i>Aglantha digitale</i>	-	-	-	-	3.7	0.3	6.0	0.9
<i>Calyropsis birulai</i>	-	-	-	-	1.2	3.0	0.4	0.1
<i>Cyanea capillata</i>	-	-	-	-	-	-	0.2	+
<i>Dimophyes arctica</i>	-	-	-	-	-	-	0.9	1.2
<i>Euphysa flammea</i>	0.4	0.1	-	-	-	-	-	-
<i>Halitholis cirratus</i>	0.5	0.3	-	-	0.1	0.5	0.1	0.4
<i>Melicertum octocostratum</i>	-	-	-	-	+	0.1	-	-
<i>Obelia longissima</i>	-	-	-	-	0.6	+	-	-
<i>Paragotoea elegans</i>	-	-	-	-	-	-	+	+
<i>Plotocnide borealis</i>	-	-	-	-	2.7	0.2	0.1	+
<i>Rhabdon reesi</i>	-	-	-	-	-	-	+	+
<i>Sarsia tubulosa</i>	0.3	0.3	-	-	0.8	2.0	-	-
<i>Sminthea arctica</i>	-	-	-	-	-	-	0.1	+
Other cnidaria	0.3	+	-	-	-	-	-	-
Amphipoda								
<i>Apherusa glacialis</i>	-	-	-	-	0.5	0.9	0.2	0.3
<i>Hyperia</i> sp.	0.6	0.6	-	-	-	-	-	-
Hyperiidæ	1.0	0.2	-	-	0.6	0.5	0.3	+
<i>Hyperoche</i> sp.	0.2	0.3	-	-	0.8	0.7	+	+
<i>Themisto abyssorum</i>	-	-	-	-	-	-	0.5	0.9
<i>Themisto libellula</i>	-	-	1.2	1.2	0.1	1.1	0.2	3.1
<i>Scina borealis</i>	-	-	-	-	-	-	+	+
Ctenophora								
<i>Beroe cucumis</i>	-	-	3.5	0.4	obs.	obs.	obs.	obs.
<i>Mertensia ovum</i>	-	-	-	-	0.6	1.0	0.2	0.2
Ostracoda								
<i>Boroecia maxima</i>	-	-	-	-	-	-	2.6	+
Pteropoda								
<i>Clione limacina</i>	-	-	-	-	-	-	0.3	0.1
<i>Limacina helicina</i>	-	-	-	-	12.9	0.1	10.0	0.1
Chaetognatha								
<i>Eukrohnia hamata</i>	-	-	-	-	-	-	4.1	0.8
<i>Parasagitta elegans</i>	9.9	2.7	28.4	4.3	132.3	19.9	63.2	6.3
<i>Pseudosagitta maxima</i>	-	-	-	-	-	-	0.1	0.2
Larvacea								
<i>Fritillaria borealis</i>	232.5	0.1	-	-	165.6	0.1	53.5	+
<i>Oikopleura vanhoeffeni</i>	277.8	14.6	118.8	11.9	73.2	0.2	75.9	0.5
Mysidae								
<i>Mysis oculata</i>	0.7	0.7	-	-	+	0.6	-	-
Euphausiidae								

<i>Thysanoessa</i> sp.	0.6	2.8	45.4	22.7	1.7	9.3	-	-
Meroplankton								
Ceriantharia	-	-	-	-	2.3	+	1.4	+
Bivalvia	-	-	4.1	+	10.5	+	4.3	+
Cirripedia	-	-	9.9	+	18.4	0.3	5.7	0.1
Decapoda	0.3	+	-	-	0.1	0.4	0.1	+
Fish larvae	-	-	-	-	0.1	3.3	-	-
Nemertina	-	-	-	-	-	-	0.3	+
Echinodermata	301.9	0.1	17.7	+	114.8	0.2	7.6	+
Polychaeta	168.3	0.8	20.0	0.1	16.7	0.2	6.4	0.1

Table 2 Pearson's correlations between log-transformed abundance data and environmental variables in the East Siberian Sea in 2015 (as presented by the BIOENV routine). S - salinity

Variables	# of variables	ρ
Sampled depth layer	1	0.63
S		0.47
Bottom depth		0.42
Sampled depth layer + Bottom depth	2	0.66
Sampled depth layer + S		0.62
S + Bottom depth		0.57
Sampled depth layer + Bottom depth + S	3	0.69

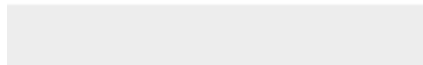
Table 3 Total zooplankton abundance, biomass, diversity and mean abundance of *Calanus glacialis* in the East Siberian Sea in 1946, 1948, 2009 and 2015 (mean \pm sd); significant interactions via the Tukey HSD test: significant interactions between years at $p < 0.05$ listed in **bold**; non-bold interactions indicate significance at $p < 0.1$. Basin stations with depths $>200\text{m}$ were excluded from analysis

	1946 (n = 17)	1948 (n = 9)	2009 (n = 9)	2015 (n = 13)	Signif. interactions
Total abundance (ind m ⁻³)	3189 \pm 2013	1939 \pm 2116	7091 \pm 6940	2908 \pm 1950	2009 > 1946, 1948
Total biomass (mg DW m ⁻³)	25 \pm 24	28 \pm 44	54 \pm 23	35 \pm 16	2009 > 1946, 1948; 2015 > 1948
<i>Calanus glacialis</i> (ind m ⁻³)	14 \pm 21	83 \pm 231	147 \pm 181	163 \pm 172	2009, 2015 > 1946, 1948
Number of taxa recorded	28	20	41	70	



[Click here to access/download](#)

Electronic Supplementary Material
Electronic Supplementary Material 1.pdf





[Click here to access/download](#)

Electronic Supplementary Material
Electronic Supplementary Material 2.docx

