1   **Cross-shelf structure and distribution of mesozooplankton communities in the East-**

2   **Siberian Sea and the adjacent Arctic Ocean**

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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

Introduction

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

Despite much effort being devoted to Arctic research in recent decades, mostly it has been concentrated in relatively easily accessible regions within the European and north-American sectors (e.g. Kassens et al. 1999; Stein et al. 2003; Flint et al. 2010; Grebmeier and Maslowski 2014). The large knowledge gaps remain primarily along the Siberian shelf, despite its high significance for sea ice formation and ocean circulation within the Arctic. Due to its remote location, shallow depths inaccessible to large research vessels, and historically servere ice conditions, the ESS remains the most understudied of all Arctic shelves, even compared to other Russian Arctic seas, with the few existing studies in western literature limited to oceanography and biogeochemistry (i.e., Münchow et al. 1999; Semiletov et al. 2005; Anderson et al. 2011; Pipko et al. 2011). Limited information on the East Siberian shelf pelagic biological communities collected in the 1940's, and 1980's was published in Russian "grey" literature (Brodsky 1957; Pavshtiks 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   (SeaBirdTM 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 Pavshtiks (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-µm double ring net of 60-cm mouth diameter,
136 with flowmeters attached at the mouth, towed vertically from ~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-µm 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 (α = 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   (Dufrêne 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**

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 µg L^{-1}. Within the surface

201   mixed layer they rarely exceeded 0.2-0.4 µg 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 *Calycopsis 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 ρ = 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 allochtonous 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 expatrites
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

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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

Compliance with Ethical Standards

The authors declare that the research was conducted in the absence of any commercial or

financial relationships that could be construed as a potential conflict of interest.

586

Figure 1

(a) Transect 1

(b) Transect 2

Figure 3

(a) Species diversity

(b) Abundance (ind m^{-3})

(c) Biomass (mg DW m^{-3})

Depth

Distance [km]

Distance [km]

Transect 1

Transect 2
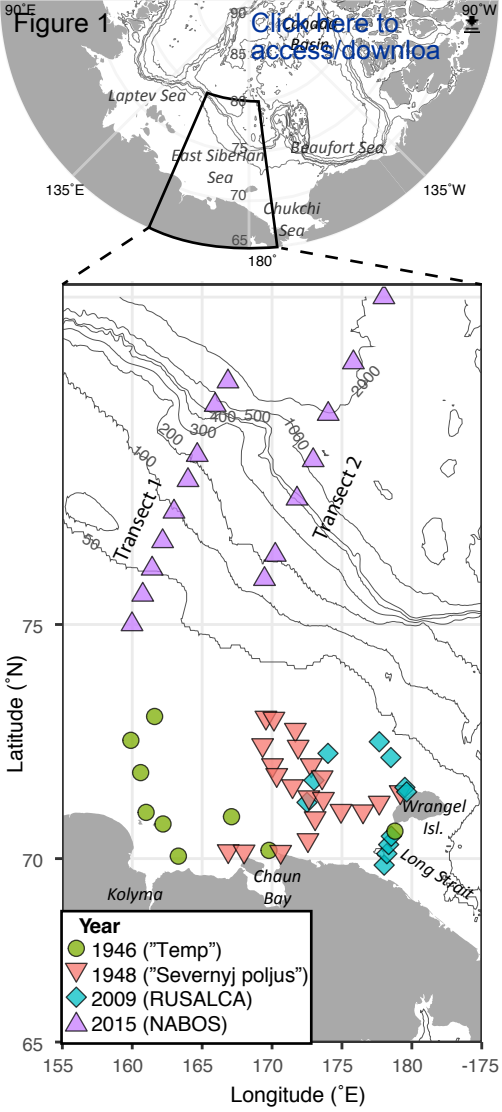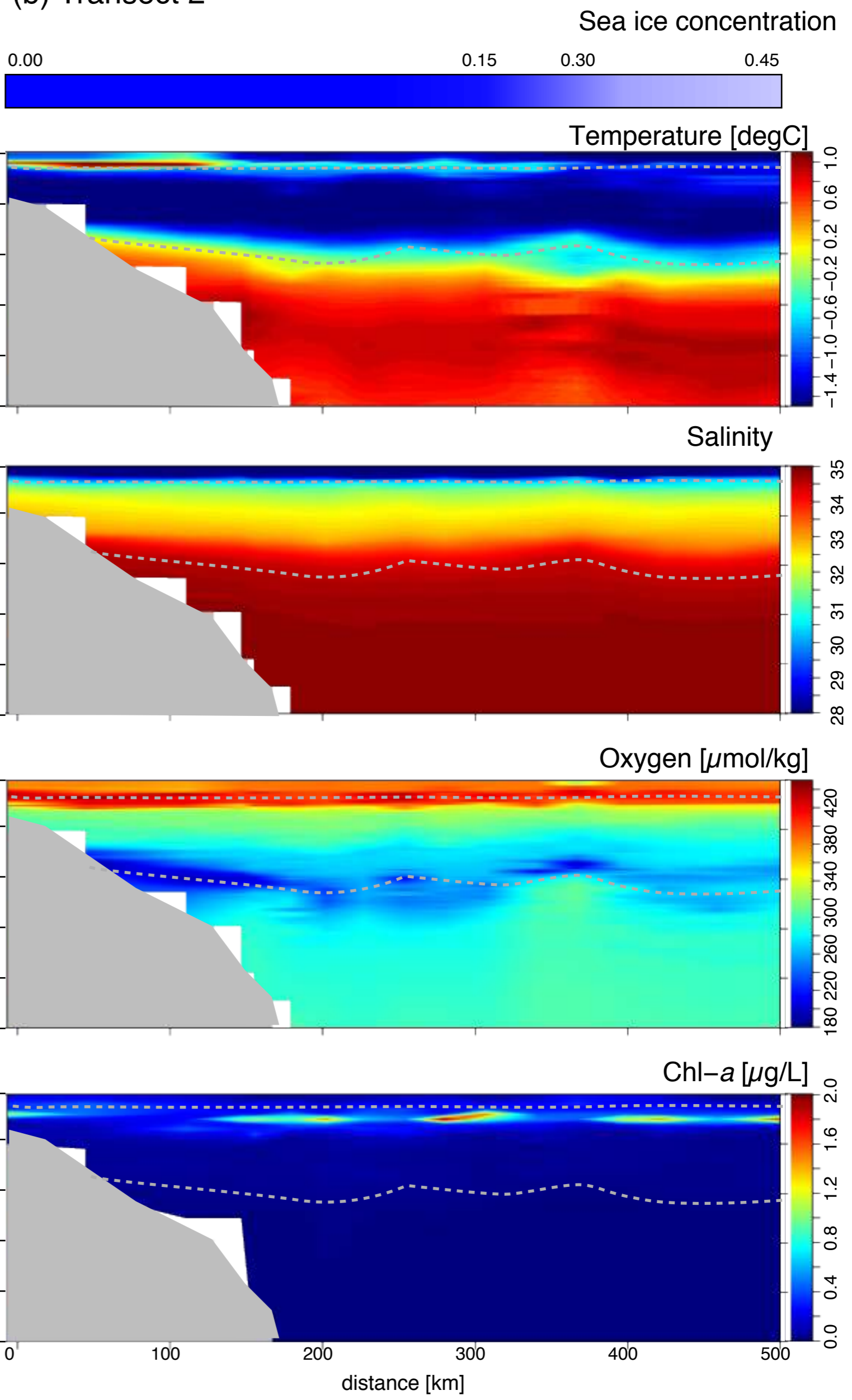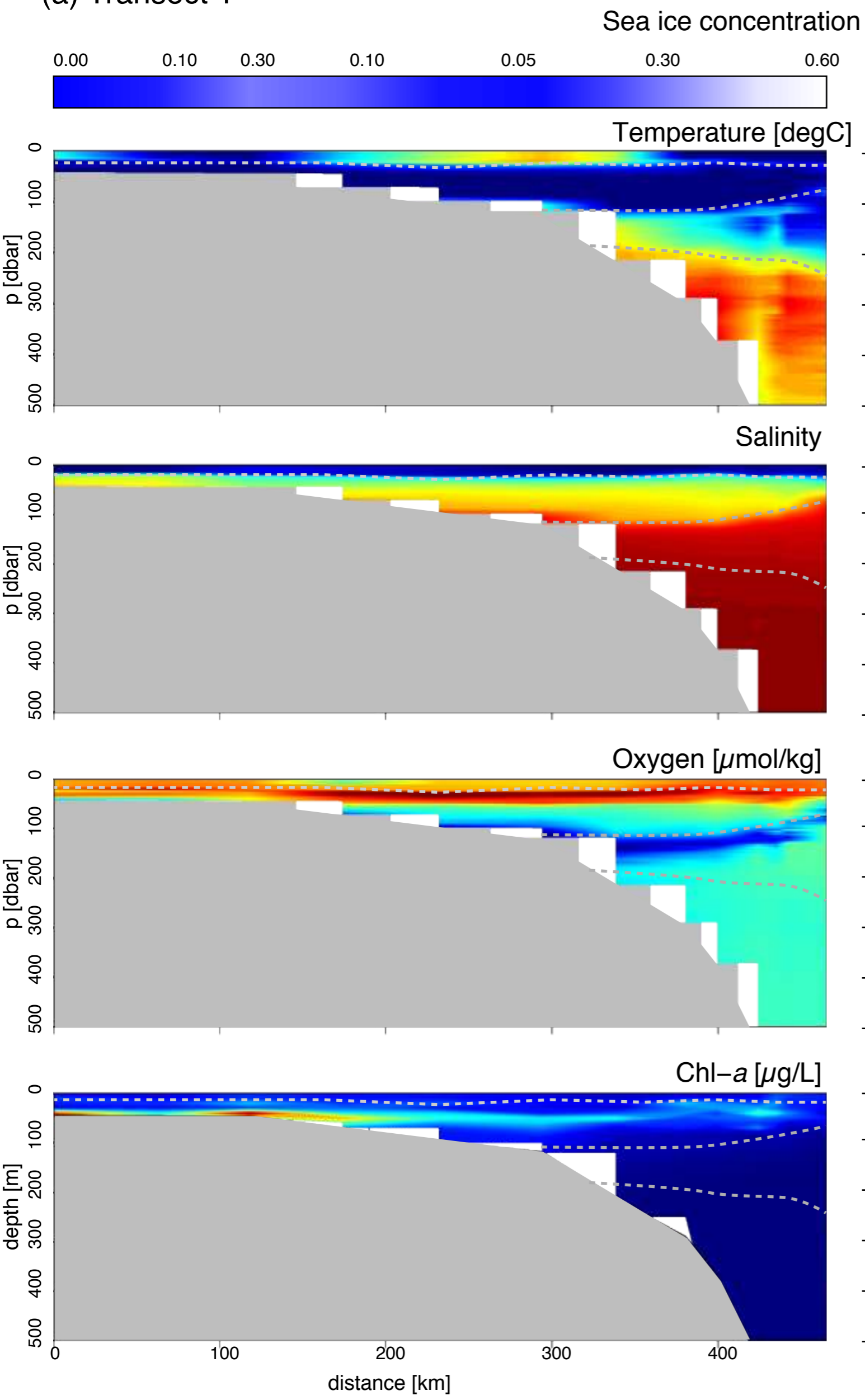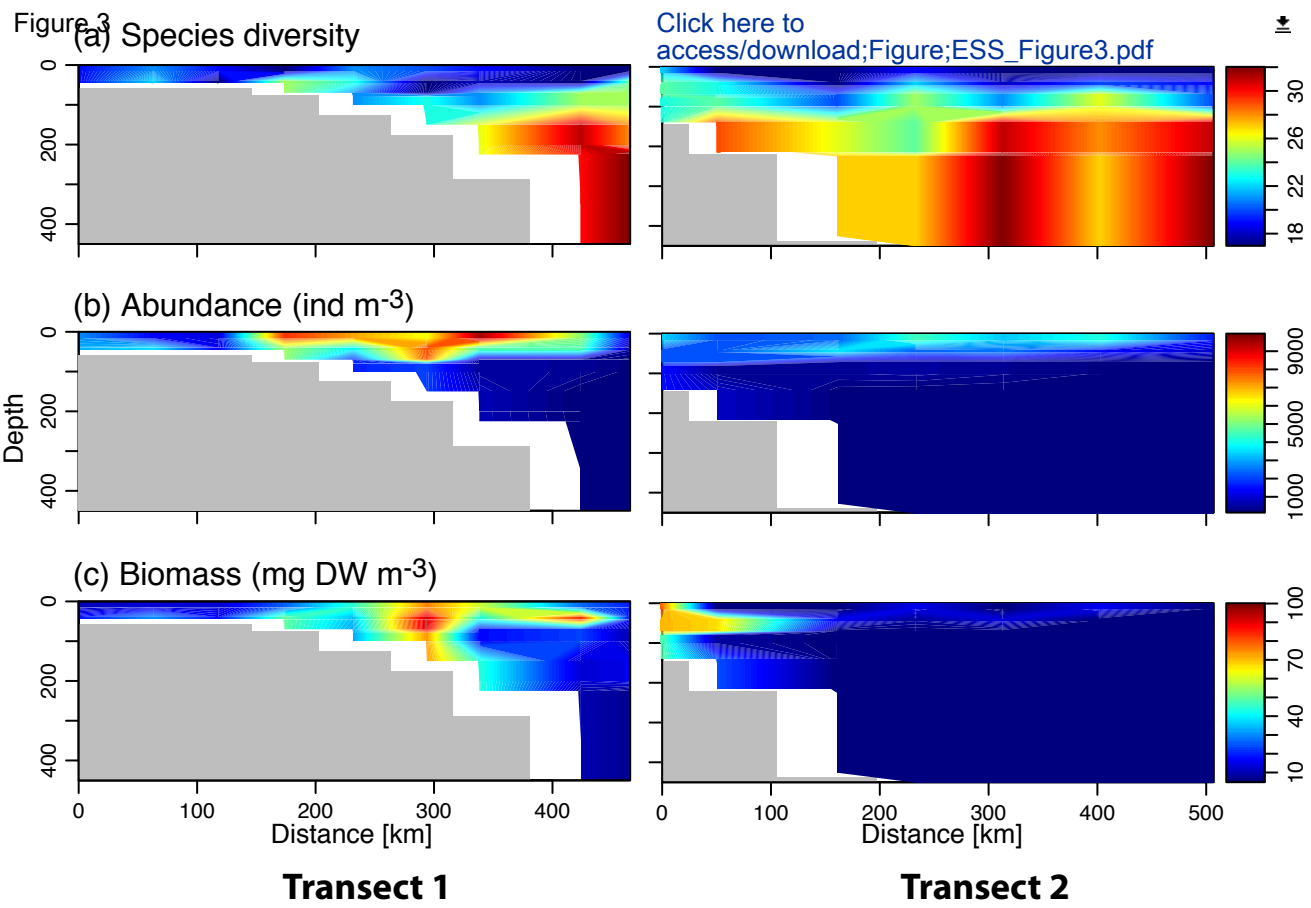
Figure 5

Figure 7

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.

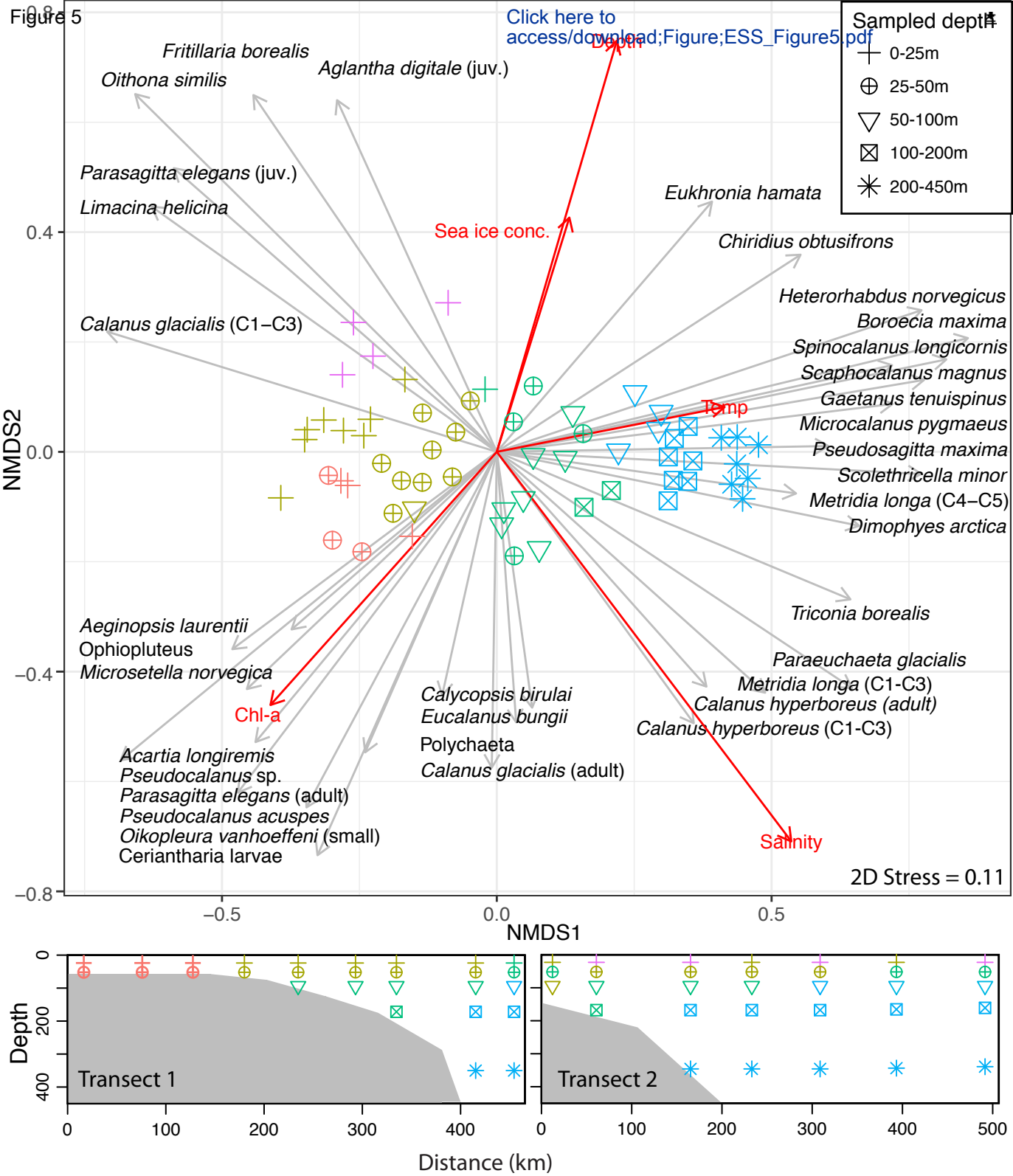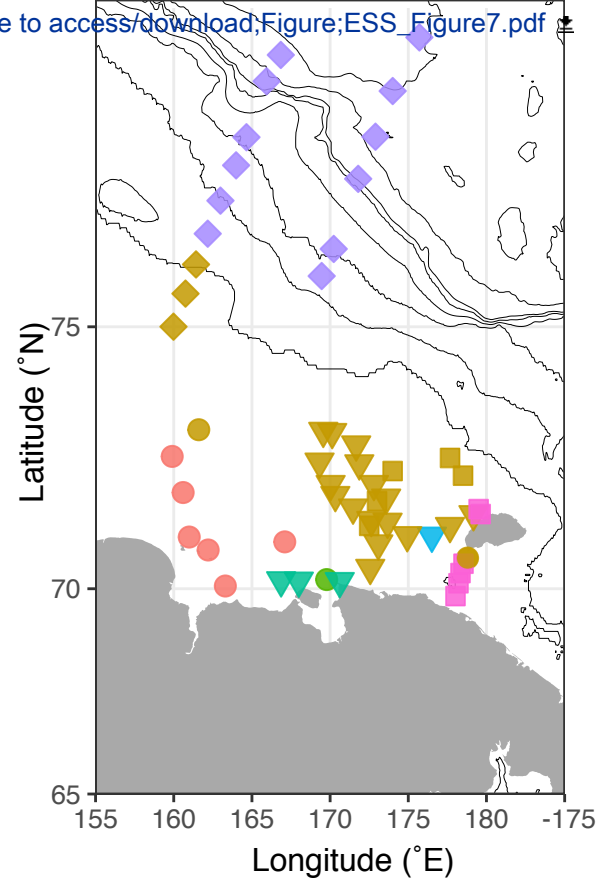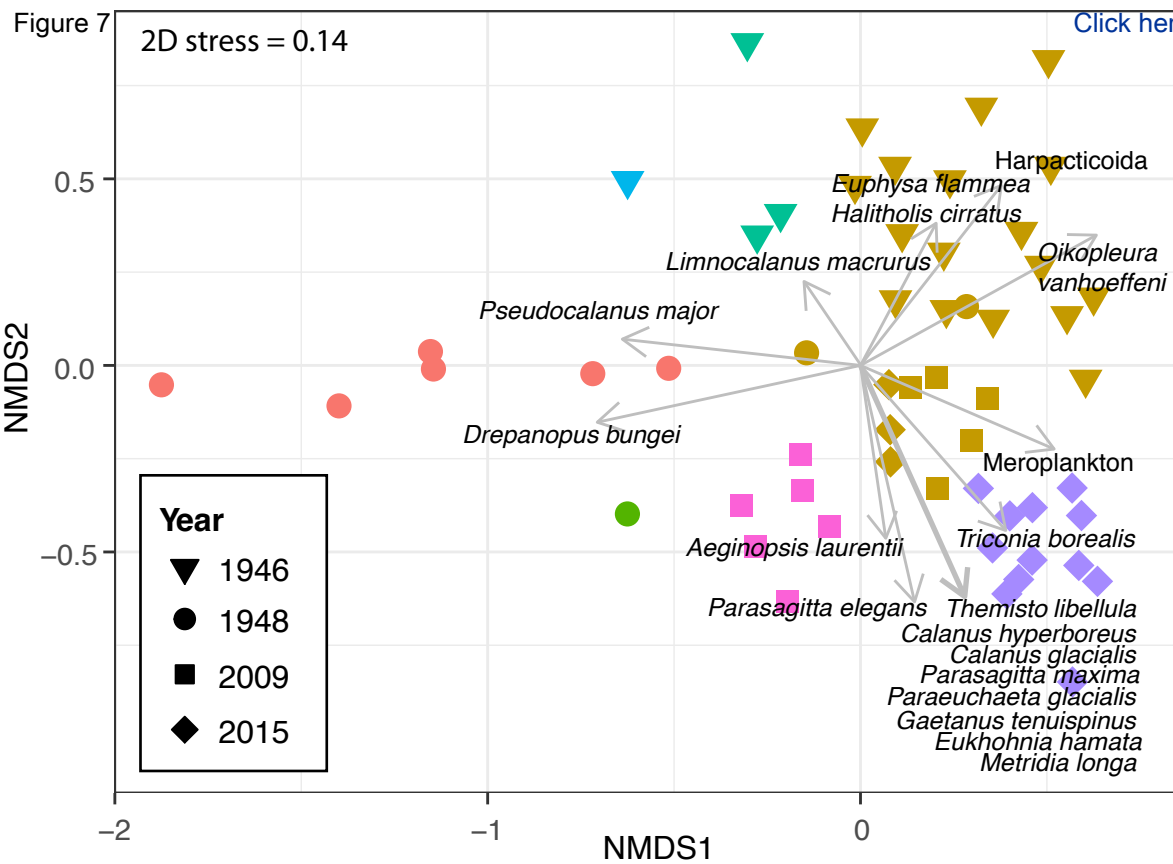| Species	1946 (data from Markhaseva et al. 2005)		1948 (Pavshtiks, 1994)		2009 (Ershova et al., 2015a)		2015 (This study)	
	Abund.	Biom.*	Abund.	Biom.*	Abund.	Biom.	**Abund.**	**Biom.**
Copepoda								
Acartia longiremis	75.9	0.4	19.8	0.1	36.1	0.1	**4.8**	**+**
Aetideopsis rostrata	-	-	-	-	-	-	**0.3**	**+**
Bradyidius similis	-	-	-	-	-	-	**4.0**	**0.1**
Aetideidae	-	-	-	-	-	-	**0.2**	**+**
Calanus finmarchicus	-	-	-	-	-	-	**0.6**	**0.1**
Calanus glacialis	17.9	1.5	106.9	16.0	147.3	10.6	**75.1**	**8.8**
Calanus hyperboreus	-	-	-	-	0.1	0.3	**7.0**	**3.7**
Chiridius obtusifrons	-	-	-	-	-	-	**0.8**	**0.2**
Disco triangularis	-	-	-	-	-	-	**0.2**	**0.3**
Drepanopus bungei	-	-	871.3	2.2	-	-	**-**	**-**
Eucalanus bungii	0.4	0.1	-	-	-	-	**0.3**	**0.1**
Eurytemora herdmani	-	-	-	-	-	-	**1.1**	**+**
Gaetanus brevispinus	-	-	-	-	-	-	**+**	**+**
Gaetanus tenuispinus	-	-	-	-	1.0	0.1	**1.2**	**0.2**
Heterorhabdus norvegicus	-	-	-	-	-	-	**1.0**	**0.1**
Jaschnovia brevis	-	-	-	-	-	-	**10.1**	**0.2**
Jaschnovia tolli	24.7	1.9	31.9	1.0	-	-	**0.6**	**+**
Jaschnovia sp.	-	-	-	-	-	-	**1.3**	**+**
Limnocalanus macrurus	3.7	+	-	-	-	-	**-**	**-**
Metridia longa	-	-	-	-	6.8	0.9	**30.3**	**1.9**
Metridia pacifica	-	-	-	-	-	-	**1.2**	**0.2**
Microcalanus pygmaeus	67.1	0.1	19.8	+	1.3	+	**34.2**	**0.1**
Microsetella norvegica	-	-	-	-	123.1	0.9	**4.1**	**+**
Paraeuchaeta glacialis	-	-	-	-	-	-	**0.9**	**0.6**
Paraeuchaeta barbata	-	-	-	-	-	-	**+**	**+**
Paraeuchaeta polaris	-	-	-	-	-	-	**+**	**+**
Paraheterorhabdus compactus	-	-	-	-	-	-	**+**	**+**
Pseudocalanus newmani	-	-	-	-	-	-	**4.0**	**+**
Pseudocalanus acuspes	-	-	-	-	26.8	0.3	**38.6**	**0.3**
Pseudocalanus major	13.8	0.1	119.4	0.3	-	-	**-**	**-**
Pseudocalanus minutus	-	-	-	-	3.6	0.1	**30.8**	**0.3**
Pseudocalanus sp.	913.7	2.3	285.5	0.7	4331.8	10.3	**1140.8**	**3.4**
Scaphocalanus brevicornis	-	-	-	-	-	-	**+**	**+**
Scaphocalanus magnus	-	-	-	-	-	-	**0.4**	**0.2**
Scolethricella minor	-	-	-	-	-	-	**1.1**	**+**
Spinocalanus antarcticus	-	-	-	-	-	-	**+**	**+**
Spinocalanus longicornis	-	-	-	-	-	-	**5.6**	**+**
Temorites brevis	-	-	-	-	-	-	**+**	**+**
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**
Oithona similis	411.9	0.6	225.7	0.3	1836.7	2.7	**653.0**	**0.7**
Triconia borealis	60.8	0.1	-	-	0.2	+	**37.7**	**0.1**
Cyclopoida	-	-	-	-	-	-	**0.5**	**+**
Cnidaria								
Aeginopsis laurentii	2.5	0.1	2.6	0.1	8.2	0.2	**3.9**	**0.1**
Aglantha digitale	-	-	-	-	3.7	0.3	**6.0**	**0.9**
Calycopsis birulai	-	-	-	-	1.2	3.0	**0.4**	**0.1**
Cyanea capillata	-	-	-	-	-	-	**0.2**	**+**
Dimophyes arctica	-	-	-	-	-	-	**0.9**	**1.2**
Euphysa flammea	0.4	0.1	-	-	-	-	**-**	**-**
Halitholis cirratus	0.5	0.3	-	-	0.1	0.5	**0.1**	**0.4**
Melicertum octocostratum	-	-	-	-	+	0.1	**-**	**-**
Obelia longissima	-	-	-	-	0.6	+	**-**	**-**
Paragotoea elegans	-	-	-	-	-	-	**+**	**+**
Plotocnide borealis	-	-	-	-	2.7	0.2	**0.1**	**+**
Rhabdon reesi	-	-	-	-	-	-	**+**	**+**
Sarsia tubulosa	0.3	0.3	-	-	0.8	2.0	**-**	**-**
Sminthea arctica	-	-	-	-	-	-	**0.1**	**+**
Other cnidaria	0.3	+	-	-	-	-	**-**	**-**
Amphipoda								
Apherusa glacialis	-	-	-	-	0.5	0.9	**0.2**	**0.3**
Hyperia sp.	0.6	0.6	-	-	-	-	**-**	**-**
Hyperiidae	1.0	0.2	-	-	0.6	0.5	**0.3**	**+**
Hyperoche sp.	0.2	0.3	-	-	0.8	0.7	**+**	**+**
Themisto abyssorum	-	-	-	-	-	-	**0.5**	**0.9**
Themisto libellula	-	-	1.2	1.2	0.1	1.1	**0.2**	**3.1**
Scina borealis	-	-	-	-	-	-	**+**	**+**
Ctenophora								
Beroe cucumis	-	-	3.5	0.4	obs.	obs.	**obs.**	**obs.**
Mertensia ovum	-	-	-	-	0.6	1.0	**0.2**	**0.2**
Ostracoda								
Boroecia maxima	-	-	-	-	-	-	**2.6**	**+**
Pteropoda								
Clione limacina	-	-	-	-	-	-	**0.3**	**0.1**
Limacina helicina	-	-	-	-	12.9	0.1	**10.0**	**0.1**
Chaetognatha								
Eukrohnia hamata	-	-	-	-	-	-	**4.1**	**0.8**
Parasagitta elegans	9.9	2.7	28.4	4.3	132.3	19.9	**63.2**	**6.3**
Pseudosagitta maxima	-	-	-	-	-	-	**0.1**	**0.2**
Larvacea								
Fritillaria borealis	232.5	0.1	-	-	165.6	0.1	**53.5**	**+**
Oikopleura vanhoeffeni	277.8	14.6	118.8	11.9	73.2	0.2	**75.9**	**0.5**
Mysidae								
Mysis oculata	0.7	0.7	-	-	+	0.6	**-**	**-**
Euphausiidae								

Thysanoessa 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 ± 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 >200m were excluded from analysis

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

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