



Title	Yearly comparison of the planktonic chaetognath community in the Chukchi Sea in the summers of 1991 and 2007
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1 Yearly comparison of the planktonic chaetognath community in the Chukchi Sea in the summers of
2 1991 and 2007

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13 **Abstract**

14 In oceans worldwide, chaetognaths are the second most dominant zooplankton taxa and have vital
15 transfer roles between herbivores and higher trophic organisms. Despite the chaetognaths'
16 importance, little is known regarding their ecology in the Chukchi Sea, where recent ice reduction is
17 prominent in the Arctic Ocean. We made comparisons of the chaetognath abundance, biomass,
18 community structure (total length and gonadal maturation) and feeding impacts between the years
19 1991 and 2007. Within the chaetognath community, *Parasagitta elegans* was the abundant species,
20 and *Eukrohnia hamata* only occurred in the southern region in 2007. Yearly differences were
21 detected in chaetognath abundance, biomass, total length and gonadal maturation. All of these
22 parameters were greater and more advanced in 1991 than in 2007. The most prominent yearly
23 differences were in the horizontal distributions of chaetognaths, primarily in the northern region in
24 1991 and the southern region in 2007. The southern chaetognath populations observed in 2007 were
25 considered to be transported by the Pacific water through the Bering Strait. Because of the
26 differences in the original populations between the Chukchi Sea in 1991 and the Bering Sea in 2007,
27 differences in these two years may be due to regional differences. As the Arctic warms, the
28 horizontal distribution pattern, similar with 2007 in this study, will be more pronounced.

29 **Keywords:**

30 chaetognaths, *Parasagitta elegans*, *Eukrohnia hamata*, Chukchi Sea

31 **1. Introduction**

32 Due to the effect of global warming, faster ice melting times and larger open water areas have recently
33 been observed in the Arctic Ocean (cf. Perovich, 2011). Within the Arctic Ocean, the effect of ice
34 reduction is prominent in the Chukchi Sea because of the intrusion of warm Pacific water (Pisareva et
35 al., 2015). The evaluation of the effects of such environmental changes on marine ecosystems is of
36 prime importance. As changes occur in the marine ecosystem, shifts in the northern zooplankton
37 community, increases in the transport of Pacific copepods to the Arctic Ocean, late phytoplankton
38 bloom timing, decreases in bloom magnitude, and potential mismatches between primary production
39 and the reproduction of copepods have been reported (Søreide et al., 2010; Matsuno et al., 2011;
40 Grebmeier, 2012; Fujiwara et al., 2014). However, little is known regarding the effect on carnivorous
41 planktonic chaetognaths.

42 Chaetognaths are reported to have the second largest zooplankton biomass after copepods
43 worldwide (Terazaki, 1998). Chaetognaths feed mainly on copepods (Pearre, 1981; Øresland, 1987)
44 and are fed upon by higher trophic level organisms (e.g., fishes). In the Chukchi Sea, the chaetognath
45 community is dominated by *Parasagitta elegans* composing 90-100% both in abundance and biomass
46 with the mesopelagic *Eukrohnia hamata* being reported much less frequency (Hopcroft et al., 2010;
47 Eisner et al., 2013; Questel et al., 2013; Ershova et al., 2015; Pinchuk and Eisner, 2017). The biomass
48 of *P. elegans* is dominant in the Chukchi zooplankton community, followed by the copepod *Calanus*
49 *glacialis*, and ranges from 0.13 to 1.80 times the biomass of *C. glacialis* (Questel et al., 2013).
50 Furthermore, the chaetognath *P. elegans* along with a diverse assemblage of cnidarians comprised the
51 dominant predators in the Chukchi Sea (Hopcroft et al, 2010). Though important, little information
52 is available about the ecology and effects of climate/environmental changes on chaetognaths in the
53 Chukchi Sea.

54 In this study, we made a yearly comparison of the summer chaetognath community on the

55 Chukchi Sea shelf region between two years, 1991 and 2007. These years correspond to before
56 (1991) and after (2007) the onset of large-scale ice reduction in summer (Walsh, 2013). The
57 transportation of Pacific water in 2007 is reported to be the largest on record (Woodgate et al., 2010).
58 We quantified the chaetognath abundance, biomass, body size, population structure and feeding impact
59 in both years (1991 and 2007) and evaluated the effects of environmental changes on the chaetognath
60 community.

61 **2. Materials and methods**

62 *2.1. Field sampling*

63 During two cruises of the T/S *Oshoro-Maru* (OS91-38th and OS07-180th), zooplankton samplings
64 were performed by vertical tows of a NORPAC net (mouth diameter 45 cm, mesh size 0.335 mm;
65 Motoda, 1957) at 1 m s⁻¹ from 5 m above the bottom to the surface at the 26 stations (1991) and 31
66 stations (2007) located at 66°10'-71°04'N and 162°02'-168°55'W over the Chukchi Sea shelf during
67 24-31 July 1991 and 5-13 August 2007 (Fig. 1). Details of the positions, local times and depths of
68 the sampling stations are shown in the Appendix. Sunset and sunrise were at approximately 00:30
69 and 04:00 local time, respectively. Sampling was undertaken both day and night. In total, there
70 were 50 daytime stations and 7 night stations. A flowmeter (Rigo Co. Ltd., Saitama, Japan) was
71 mounted on the net ring to register the filtered volume. Zooplankton samples were preserved in 5%
72 borax-buffered formalin seawater immediately after collection. The temperature and salinity at each
73 station were measured by a Conductivity, Temperature, Depth profiler (CTD) (Neil Brown Inc., Mark
74 3B in 1991, Sea-Bird Electronics Inc., SBE 911 Plus in 2007). From the T-S diagrams, water mass
75 separation was made using criteria from Danielson et al. (2017).

76 *2.2. Sample analysis*

77 In the laboratory, zooplankton samples were divided into half aliquots using a Motoda splitter (Motoda,
78 1959). One aliquot was used for wet weight measurements, and the others were used for microscopic
79 examination. For the wet weight measurement, zooplankton samples were filtered through a pre-
80 weighed 100 µm mesh; the seawater was then removed with the aid of tissue, and their weights were
81 measured with a microbalance (Mettler PM4000) to a precision of 0.01 g.

82 Chaetognaths in the remaining half aliquots were sorted and identified to species under a
83 stereomicroscope. The total lengths (TL, mm), from the top of the head to the end of the body
84 without the caudal fin, of the dominant chaetognaths *P. elegans* and *E. hamata* were measured by
85 callipers for large specimens (TL ≥ 10 mm) or an eye-piece micrometer for small specimens (TL < 10
86 mm) to a precision of 0.1 mm. Based on gonadal maturation, *P. elegans* was classified into five
87 stages: juvenile and stages I, II, III, and IV (Thomson, 1947; Terazaki and Miller, 1986; Johnson and
88 Terazaki, 2003). *E. hamata* was classified into eight stages: juvenile and stages I-VII (Kosobokova
89 and Isachenko, 2017). Dry mass (DM, µg ind.⁻¹) and biomass were calculated from the TL using the
90 following equations:

91 $E. hamata: \text{Log}_{10} \text{DM} = 3.80 \text{Log}_{10} \text{TL} - 0.79$ (Matsumoto, 2008)

92 $P. elegans: \text{Log}_{10} \text{DM} = 2.91 \text{Log}_{10} \text{TL} - 0.79$ (Nakamura et al., 2017).

93 The gut contents of the dominant chaetognath, *P. elegans*, were identified to species and counted
94 separately from the empty guts. For calanoid copepods in the guts, identification was made to stages,
95 if possible. To evaluate the feeding impact of *P. elegans*, the number of prey per chaetognath (NPC)
96 values were calculated (Nagasawa and Marumo, 1972). The feeding rate (FR: number of prey
97 consumed ind.⁻¹ day⁻¹) was calculated with the following equation:

98
$$\text{FR} = \text{NPC} \times 24/\text{DT}$$

99 where DT indicates digestion time (hours) and was calculated with following equation (Pearre, 1981):

100
$$\text{DT} = 10.24e^{-0.095T}$$

101 where T indicates the integrated mean temperature of the sampling depths (°C). The feeding impact
102 (no. of prey m⁻³ day⁻¹) was calculated by multiplying FR and *P. elegans* abundance (ind. m⁻³). By
103 applying the calanoid copepod abundance data from the same zooplankton samples (Matsuno et al.,
104 2011), the daily feeding impact of *P. elegans* (% day⁻¹) was also calculated.

105 2.3. Statistical analysis

106 A cohort analysis was made of *P. elegans* TL data with the aid of Microsoft Excel Solver (Aizawa and
107 Takiguchi, 1999). Because of the low abundance of *E. hamata*, no cohort analysis was made of this
108 species. Yearly differences in environmental parameters (temperature, salinity), zooplankton
109 (abundance, biomass), copepods (abundance), chaetognaths (abundance, biomass, mean TL and
110 population structure) were tested by *U*-test. To evaluate the factors governing chaetognath (*P.*
111 *elegans*) abundance, a structural equation modelling (SEM) analysis was made for each year. For
112 the SEM analysis, we analysed the correlations between *P. elegans* abundance and geographic
113 parameters (latitude, longitude, depth), environmental parameters (integrated mean temperature and
114 salinity) or biological parameters (abundances of small copepods, large copepods and Pacific
115 copepods). Pacific copepods were defined as the following: *Neocalanus cristatus*, *N. flemingeri*, *N.*
116 *plumchrus*, *Eucalanus bungii* and *Metridia pacifica*. *Calanus glacialis* and *C. hyperboreus* were
117 considered large copepods. Small copepods included the remaining species, mainly *Pseudocalanus*
118 spp. All these copepod data are from Matsuno et al. (2011).

119 3. Results

120 3.1. Hydrography

121 In 1991, the integrated mean temperature and salinity ranged from 0.9 to 7.2°C and 29.2 to 32.3,
122 respectively (Fig. 2a, b). High temperature with less saline water was seen along the Alaskan coast.

123 In 2007, the integrated mean temperature was 3.1–10.6°C, and the salinity was 31.1–32.9. The
124 yearly comparisons revealed that 2007 was characterised by higher temperatures and salinities than
125 1991. The plotted positions on the T-S diagram also varied greatly by year. Thus, the surface water
126 was mainly composed of meltwater (MW) in 1991 and was dominated by the Alaskan Coastal Water
127 (ACW) in 2007 (Fig. 2c). The bottom water was composed of the Bering-Chukchi Winter Water
128 (BCWW) in 1991 and was dominated by the Bering-Chukchi Summer Water (BCSW) in 2007.

129 3.2. *Chaetognath abundance and biomass*

130 In 1991, the chaetognath abundance was 177–1952 ind. m⁻² at the sampled stations (mean: 818 ind.
131 m⁻²) and was high north of the Lisburne Peninsula (Fig. 3a). The biomass was 30.9–451.0 mg DM
132 m⁻² (mean: 160.8 mg DM m⁻²) and was also high north of the Lisburne Peninsula (Fig. 3b). In 2007,
133 the chaetognath abundance was 0–2491 ind. m⁻² (mean: 474 ind. m⁻²) and was high south of the
134 Lisburne Peninsula. Biomass ranged from 0–388.5 mg DM m⁻² (mean: 78.6 mg DM m⁻²) and was
135 also high south of the Lisburne Peninsula. Within the chaetognath community, *P. elegans* was
136 predominant in both years, comprising 100% (1991) or 95.5% (2007) of the cumulative catch. *E.*
137 *hamata* only occurred south of the Lisburne Peninsula in 2007 to a limited extent (6–65 ind. m⁻² or
138 4.6–241.0 mg DM m⁻²) (Fig. 1).

139 3.3. *Total length and population structure*

140 For both years, no spatial changes in TL and population structure were detected. We pooled them
141 and showed the cumulative data for each year.

142 In 1991, the TL of *P. elegans* ranged from 1.0–26.3 mm (Fig. 4). The TLs of each stage
143 were as follows: Juvenile, 1.0–19.4 mm; Stage I, 9.4–22.4 mm; Stage II, 15.1–26.3 mm; Stage III,
144 16.1–25.9 mm. The TL histogram based on the cumulative data for the whole station clearly

145 separated into two cohorts. The mean TL of the small cohort was 4.1 mm and was mainly composed
146 of Juveniles, and the mean TL of the large cohort was 15.4 mm and composed of Stage I.

147 In 2007, the TL of *P. elegans* ranged from 1.7 to 29.5 mm (Fig. 4). The TLs varied with
148 the stages: Juveniles, 1.7–17.5 mm; Stage I, 9.2–24.3 mm; Stage II, 12.5–27.5 mm; Stage III, 16.4–
149 28.5 mm; Stage IV; 17.6–29.5 mm. Two cohorts were also identified for *P. elegans* in 2007.
150 However, their mean TL and compositions were very different from those in 1991. Thus, the mean
151 TL of each cohort (small: 8.3 mm, large: 20.6 mm) was larger in 2007 than in 1991. In 2007, the
152 proportion of the two cohorts was skewed for the small-sized cohort, and very few specimens belonged
153 to the large-sized cohort.

154 3.4. Food items and the predation impact of *P. elegans*

155 For *P. elegans*, a gut containing food items was seen in 34 specimens in 1991 and 47 specimens in
156 2007 (Table 1). All specimens contained one food item and no specimen had multiple prey items.
157 For most of the gut contents, species identification was difficult because of digestion. Species
158 identification was not possible for 88.2% (1991) or 83.0% (2007) of the food items. Despite such
159 limitations, the copepods *Calanus* sp., *Pseudocalanus* spp., *Pseudocalanus* spp. C2, *Pseudocalanus*
160 spp. C5F, *Pseudocalanus* spp. C6F, *Metridia pacifica* C4, *Centropages abdominalis*, and *Eurytemora*
161 *herdomani* C6 were identified as food items. For the yearly differences, *Pseudocalanus* spp.
162 dominated in 1991, while *E. herdomani* dominated and was only seen in 2007.

163 For *P. elegans*, the number of prey per chaetognath (NPC) was 0.035 (3.5%) in 1991 and
164 0.045 (4.5%) in 2007. The feeding impact was calculated as 155.4 prey m⁻² day⁻¹ in 1991 and 249.4
165 prey m⁻² day⁻¹ in 2007. The daily feeding impact on the copepod community was 1.2% day⁻¹ in 1991
166 and 0.7% day⁻¹ in 2007.

167 3.5. SEM analysis

168 From the SEM analysis, the *P. elegans* abundance in 1991 showed that they were positively affected
169 by the depth, integrated mean temperature, salinity and large-sized copepods and negatively affected
170 by small copepods (Fig. 5). On the other hand, the *P. elegans* abundance in 2007 had fewer
171 interactions with the geographical, environmental and biological parameters. Latitude had negative
172 effects and small copepods had positive effects on *P. elegans* abundance, while their path coefficient
173 values were low.

174 **4. Discussion**

175 4.1. Methodological note

176 The most important methodological note of this study is that all the samplings were undertaken in the
177 Arctic summer, which is characterised by the midnight sun. *P. elegans* is known to perform vertical
178 diel migrations; in particular, large individuals remain in the deeper layers during the daytime (Zo,
179 1973; King, 1979; Conway and Williams, 1986). The water depths of the sampling stations of this
180 study were all shallower than 50 m (Fig. 1). Under midnight sun conditions, *P. elegans* would be
181 expected to be distributed around the near-bottom layer at each station. A near-bottom aggregation
182 of chaetognaths has been reported from oceans worldwide (Cartes, 1998; Ozawa et al., 2004). Since
183 the samplings of this study were made by vertical hauls from the bottom 5 m, the possibility that we
184 failed to collect near-bottom aggregates of *P. elegans* cannot be denied.

185 A diel feeding rhythm (nocturnal feeding) is also reported for *P. elegans* (Øresland, 1987;
186 Terazaki, 1995). Bearing this in mind, the feeding intensity of *P. elegans* in this study is expected to
187 be low under the midnight sun condition. This could be a possible cause of the low NPC of this study
188 (0.035–0.045) compared with the reported values for *P. elegans* (0.4–0.9; Øresland, 1987; Tønnesson
189 and Tiselius, 2005). Thus, the midnight sun condition of this study may have the possibility of a

190 near-bottom distribution and a low *P. elegans* feeding intensity. These facts may have resulted in the
191 collection of few large-sized (Fig. 4) and few food-containing individuals (Table 1) of *P. elegans* in
192 this study. While these shortcomings are present, information on species occurring as prey of *P.*
193 *elegans* are valuable. Within them, copepods *C. abdominalis* and *E. herdmani* are the first record
194 as prey for *P. elegans* (cf. Terazaki, 1998). Since both species are categorized as neritic species
195 (Brodsky, 1967), it is expected that they would be included in the shallow depth region (<50 m) of this
196 study (Fig. 1).

197 4.2. Horizontal distribution of chaetognaths

198 *E. hamata* is the dominant mesopelagic chaetognath in the Arctic basin (Kosobokova et al., 1998;
199 Kosobokova and Hirche, 2000; Grigor et al., 2017). Since the sampling depths of this study were
200 shallower than 50 m, the low occurrence of *E. hamata* in this study is primarily due to the shallower
201 sampling depths. On the other hand, *P. elegans* dominates the chaetognath fauna on the Arctic
202 shelves (Grigor et al., 2014). In the present study, *P. elegans* was the only chaetognath found in 1991.
203 In contrast, *E. hamata* occurred only in 2007, especially south of the Lisburne Peninsula where it
204 bordered the Bering Strait (Fig. 1). In 2007, the area where *E. hamata* occurred corresponded to the
205 observed high abundance of *P. elegans* (Figs. 1 and 3). As the *E. hamata* occurred around southern
206 Chukchi Sea, Pinchuk and Eisner (2017) considered that they are transported from Pacific water, and
207 treated as seven large-bodied taxa originating from deep Pacific water which including copepods *N.*
208 *cristatus*, *N. flemingeri*, *N. plumchrus*, *E. bungii*, *M. pacifica*, hyperid amphipod *Themisto pacifica*
209 and chaetognath *E. hamata*. From this point of view, both *P. elegans* and *E. hamata* in the south of
210 Lisburne Peninsula in 2007 were transported by the Pacific water passing through the Bering Strait.

211 Chaetognaths are treated as water mass indicator species (cf. Pierrot-Bults, 2008). The
212 surface and bottom water masses throughout the study area in 2007 were dominated by the ACW and

213 BCSW, respectively (Fig. 2c). While the whole area was covered by the same water masses (ACW
214 and BCSW), horizontal gradients of *E. hamata* distribution and a high abundance of *P. elegans* south
215 of the Lisburne Peninsula area were prominent. The amount of Pacific water transported through the
216 Bering Strait was reported to be highest in 2007 (Woodgate et al., 2010). These facts suggest that
217 the amounts of transported chaetognaths originating in the Pacific were also high in 2007. In the
218 Chukchi Sea, the dominant pelagic fish is age-0 Arctic cod (*Boreogadus saida*) (De Robertis et al.,
219 2017). Chaetognaths are reported to be prey of Arctic cod and composed 1.2-8.7% in weight of prey
220 (Buckley and Whitehouse, 2017). Through northward transport of the Pacific chaetognaths, they
221 may suffer such high predation pressure by Arctic cod. It may be a possible cause of the low
222 abundance of chaetognaths in the north of Lisburne Peninsula in 2007.

223 The horizontal advection of Pacific chaetognaths in 2007 may explain why the bottom-up
224 (geographical, environmental and biological) parameters of SEM analysis were not suitable for this
225 year (Fig. 5). Small copepods showed positive correlation, but the coefficient value was low (0.25).
226 It also should be noted that feeding on neritic copepods (*C. abdominalis* and *E. herdomani*) was
227 observed only in 2007. They are included as small copepods in this study. As chaetognaths in 2007
228 may have been transported by Pacific water, no correlation with Pacific copepods seems to be
229 anomalous (Fig. 5). As mentioned above, predation by Arctic cod may explain the low abundance
230 of chaetognaths north of the Lisburne Peninsula in 2007. The predation pressure of visual feeding
231 Arctic cod is expected to be larger for the macro-sized chaetognaths than those for the meso-sized
232 copepods (Gray et al., 2016; Buckley and Whitehouse, 2017). Such taxa-specific differences in
233 predation pressure, which is related to body size, may mask the correlation between them.

234 On the other hand, because of the great regional variability in environmental parameters in
235 1991 (Fig. 2), the horizontal distribution of chaetognaths may well explain the geographical,
236 environmental and biological parameters using SEM analysis (Fig. 5). In 1991, few effects of the

237 transportation of the water mass from the Pacific showed a stable chaetognath community in this
238 region. Within the copepods (small copepods, large copepods and Pacific copepods), only small
239 copepods had correlations with chaetognaths for both years (Fig. 5). A strong negative correlation
240 in 1991 suggests that a high predation impact of *P. elegans* on small copepods was the cause of the
241 stable condition in this region.

242 As an alternative explanation of the horizontal distribution of *P. elegans* in 1991, the biomass
243 of *P. elegans* is known to exhibit strong positive correlations to salinity below the pycnocline, and
244 moderate negative correlations to temperature, indicating their affinity to BCWW and BCSW (Pinchuk
245 and Eisner, 2017). From this point of view, strong positive correlations (0.80) with integrated mean
246 salinity in 1991 of this study may confirm this horizontal distribution pattern (Fig. 5).

247 4.3. Year-to-year changes in chaetognaths

248 The yearly environmental, biological and chaetognath community differences between 1991 and 2007
249 are summarised in Table 2. Both temperature and salinity were higher in 2007 (Fig. 2c). While the
250 total zooplankton abundance and biomass did not vary with the year, the copepod abundance was
251 greater in 2007 (Table 2). This discrepancy is due to differences in the taxonomic composition of
252 the zooplankton community with barnacle larvae dominating in 1991 (Matsuno et al., 2011).

253 With optimal food conditions, growth of *P. elegans* is slow at low temperatures and fast at
254 high temperatures (Sameoto, 1971). Generation length is long at low temperatures and short at high
255 temperatures (McLaren, 1963; Sameoto, 1971). These facts suggest that the growth of *P. elegans*
256 would be faster during warm 2007. In fact, the mean TLs of both the small and large body-size
257 cohorts were larger in 2007 (Fig. 4). However, this hypothesis does not explain the great yearly
258 differences in the horizontal distribution of chaetognaths (Fig. 3). Thus, the faster growth of
259 chaetognaths in warm 2007 may not explain the phenomena in this study.

260 Chaetognaths with TL of 2-4 mm are treated as new-born in *P. elegans* (cf. Grigor et al.,
261 2017). Bearing this in mind, dominance of the 2-4 mm TL cohort in 1991 is considered recent
262 recruitment of the new generation occurring prior to the sampling date (24-31 July) (Fig. 4). In the
263 Amundsen Gulf (Beaufort Sea), two cohorts for TL in most of the year and three cohorts for TL in
264 July and August suggest that newly recruitment occurs at this season (Grigor et al., 2017). Our study
265 was conducted in July-August. While the failure to collect large body-sized individuals may have
266 been due to sampling protocol (see 4.1. Methodological note), the life cycle schema of recruitment in
267 July to August by Grigor et al. (2017) fits well with the results in 1991.

268 For the widespread chaetognath *P. elegans*, regional differences in reproduction timing, life
269 cycle and generation length are well-known (cf. Terazaki, 1998). For instance, the generation length
270 is two years in the Arctic Ocean and one year at lower latitudes (Dunbar, 1962; Pierrot-Bults, 2008).
271 At the high latitudes of the Arctic Ocean, the generation length is extended to three years (Grigor et
272 al., 2014). In contrast, two generations in one year have been reported for warm low-latitude oceans
273 (Zo, 1973). While the Chukchi and Bering seas are connected to each other, their temperatures and
274 faunas are notably different (Pisareva et al., 2015). These facts suggest that the reproduction and life
275 cycle timings of *P. elegans* may vary between the two oceans. Compared with 1991, the amount of
276 transported Pacific water through Bering Strait in 2007 is known to be the highest on record (Woodgate
277 et al., 2010). These facts suggest that the dominant chaetognaths south of the Lisburne Peninsula in
278 2007 may also be a transported expatriate community from the Bering Sea. Thus, different life-cycle
279 timings of *P. elegans* between the two oceans may be considered to provide yearly differences in body-
280 size distribution between 1991 and 2007 (Fig. 4). Differences in body-size frequency may induce
281 the yearly differences in the biomass and mean maturation stage observed in this study (Table 2).

282 **5. Conclusions**

283 Yearly comparisons of the summer chaetognath community in the Chukchi Sea between 1991 (before
284 ice melting increased) and 2007 (after ice melting increased) showed significant differences in the
285 abundance, biomass, body length and maturation of the dominant chaetognath, *P. elegans* (Table 2).
286 The horizontal distribution of *P. elegans* also varied greatly with the year: they were distributed mainly
287 north of the Lisburne Peninsula in 1991, while they were south of the Lisburne Peninsula in 2007 (Fig.
288 3). In 2007, the main distribution regions of *P. elegans* corresponded with those of *E. hamata*, which
289 were considered to be expatriated from the Pacific side through the Bering Strait (Fig. 1). These facts
290 suggest that the majority of the chaetognath community in 2007 was transported from the Bering Sea
291 (Fig. 2). The life cycle and reproduction timing of *P. elegans* are known to vary with the region.
292 Large hydrographic differences between the Chukchi Sea and Bering Sea may induce different life-
293 cycle timing in *P. elegans*. This may have produced the yearly differences between 1991 and 2007.
294 Thus, yearly differences in the *P. elegans* community may be detected by comparing originally
295 different *P. elegans* populations between the Chukchi Sea (1991) and Bering Sea (2007), since
296 differences in *P. elegans* populations between the Chukchi and Bering seas may induce yearly
297 differences in their abundance, biomass, body size and maturation between 1991 and 2007.

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306

307 **References**

- 308 Aizawa, Y., Takiguchi, N., 1999. Consideration of the methods for estimating the age-composition
309 from the length frequency data with MS Excel. Bull. Jpn. Soc. Fish. Oceanogr. 63, 205–214.
310 (in Japanese with English abstract)
- 311 Brodsky, K.A., 1967. Calanoida of the Far Eastern Seas and Polar Basin of the USSR. Israel Program
312 for Scientific Translations, Jerusalem.
- 313 Buckley, T.W., Whitehouse, G.A., 2017. Variation in the diet of Arctic Cod (*Boreogadus saida*) in the
314 Pacific Arctic and Bering Sea. Environ. Biol. Fish. 100, 421-442.
- 315 Cartes, J.E., 1998. Dynamics of the bathyal Benthic Boundary Layer in the northwestern
316 Mediterranean: depth and temporal variations in macrofaunal– megafaunal communities and
317 their possible connections within deep-sea trophic webs. Prog. Oceanogr. 41, 111-139.
- 318 Conway, D.V.P., Williams, R., 1986. Seasonal population structure, vertical distribution and migration
319 of the chaetognath *Sagitta elegans* in the Celtic Sea. Mar. Biol. 93, 377-387.
- 320 Danielson, S.L., Eisner, L., Ladd, C., Mordy, C., Sousa, L., Weingartner, T.J., 2017. A comparison
321 between late summer 2012 and 2013 water masses, macronutrients, and phytoplankton standing
322 crops in the northern Bering and Chukchi Seas. Deep-Sea Res. II 135, 7-26.
- 323 De Robertis, A., Taylor, K., Wilson, C.D., Farley, E.V., 2017. Abundance and distribution of Arctic
324 cod (*Boreogadus saida*) and other pelagic fishes over the U.S. Continental Shelf of the Northern
325 Bering and Chukchi Seas. Deep-Sea Res. II 135, 51-65.
- 326 Dunbar, M.J., 1962. The life cycle of *Sagitta elegans* in arctic and subarctic seas, and the modifying
327 effects of hydrographic differences in the environment. J. Mar. Res. 20, 76-91.
- 328 Eisner, L., Hillgruber, N., Martinson, E., Maselko, J., 2013. Pelagic fish and zooplankton species
329 assemblages in relation to water mass characteristics in the northern Bering and southeast
330 Chukchi seas. Polar Biol. 36, 87-113.

331 Ershova, E.A., Hopcroft, R.R., Kosobokova, K.N., 2015. Inter-annual variability of summer
332 mesozooplankton communities of the western Chukchi Sea: 2004-2012. *Polar Biol.* 38, 1461-
333 1481.

334 Fujiwara, A., Hirawake, T., Suzuki, K., Imai, I., Saitoh, S.I., 2014. Timing of sea ice retreat can alter
335 phytoplankton community structure in the western Arctic Ocean. *Biogeosciences* 11, 1705-
336 1716.

337 Gray, B.P., Norcross, B.L., Blanchard, A.L., Beaudreau, A.H., Seitz, A.C., 2016. Variability in the
338 summer diets of juvenile polar cod (*Boreogadus saida*) in the northeastern Chukchi and western
339 Beaufort Seas. *Polar Biol.* 39, 1069-1080.

340 Grebmeier, J. M., 2012. Shifting patterns of life in the Pacific Arctic and Sub-Arctic Seas. *Annu. Rev.*
341 *Mar. Sci.* 4, 63-78.

342 Grigor, J.J., Søreide, J. E., Varpe, Ø., 2014. Seasonal ecology and life-history strategy of the high-
343 latitude predatory zooplankton *Parasagitta elegans*. *Mar. Ecol. Prog. Ser.* 499, 77-88.

344 Grigor, J.J., Schmid, M.S., Fortier, L., 2017. Growth and reproduction of the chaetognaths *Eukrohnia*
345 *hamata* and *Parasagitta elegans* in the Canadian Arctic Ocean: capital breeding versus income
346 breeding. *J. Plankton Res.* 39, 910-929.

347 Hopcroft, R.R., Kosobokova, K.N., Pinchuk, A.I., 2010. Zooplankton community patterns in the
348 Chukchi Sea during summer 2004. *Deep-Sea Res. II* 57, 27-39.

349 Johnson, T.B., Terazaki, M., 2003. Species composition and depth distribution of chaetognaths in a
350 Kuroshio warm-core ring and Oyashio water. *J. Plankton Res.* 25, 1279–1289.

351 King, K.R., 1979. The life history and vertical distribution of the chaetognath, *Sagitta elegans*, in
352 Dabob Bay, Washington. *J. Plankton Res.* 1, 153-167.

353 Kosobokova, K.N., Hanssen, H., Hirche, H.J., Knickmeier, K., 1998. Composition and distribution of
354 zooplankton in the Laptev Sea and adjacent Nansen Basin during summer, 1993. *Polar Biol.* 19,

355 63–73.

356 Kosobokova, K.N., Hirche, H.J., 2000. Zooplankton distribution across the Lomonosov Ridge, Arctic
357 Ocean: species inventory, biomass and vertical structure. *Deep-Sea Res. I* 47, 2029–2060.

358 Kosobokova, K.N., Isachenko, A.I., 2017. The gonad maturation and size structure of the population
359 of abundant planktonic predator *Eukrohnia hamata* (Möbius, 1875) (Chaetognatha) in the
360 Eurasian basin of the Arctic Ocean in summer. *Russ. J. Mar. Biol.*, 43, 25-33.

361 Matsumoto, Y., 2008. Life cycle and production of chaetognath *Eukrohnia hamata* in the Oyashio
362 region, western North Pacific (Master thesis), Hokkaido University, Hokkaido, (in Japanese).

363 Matsuno, K., Hirawake, T., Yamaguchi, A., Imai, I., 2011. Year-to-year changes of the
364 mesozooplankton community in the Chukchi Sea during summers of 1991, 1992 and 2007,
365 2008. *Polar Biol.* 34, 1349-1360.

366 McLaren, I.A., 1963. Effects of temperature on the growth of zooplankton, and the adaptive value of
367 vertical migration. *J. Fish. Res. Bd. Can.* 20, 685–727.

368 Motoda, S., 1957. North Pacific standard plankton net. *Inform. Bull. Plankton Japan* 4, 13-15.

369 Motoda, S., 1959. Devices of simple plankton apparatus. *Mem. Fac. Fish. Hokkaido Univ.* 7, 73-94.

370 Nagasawa, S., Marumo, R., 1972. Feeding of a pelagic chaetognath, *Sagitta naga* Alvarino in Suruga
371 Bay, central Japan. *J. Oceanogr. Soc. Japan* 28, 181-186.

372 Nakamura, A. Matsuno, K., Abe, Y., Shimada, H., Yamaguchi, A., 2017. Length-weight relationships
373 and chemical composition of the dominant mesozooplankton taxa/species in the subarctic
374 Pacific, with special reference to the effect of lipid accumulation in Copepoda. *Zool. Stud.* 56,
375 13, doi:10.6620/ZS.2017.56-13.

376 Øresland, V., 1987. Feeding of the chaetognaths *Sagitta elegans* and *S. setosa* at different seasons in
377 Gullmarsfjorden, Sweden. *Mar. Ecol. Prog. Ser.* 39, 69-79.

378 Ozawa, M., Yamaguchi, A., Kitamura, M., 2004. Small scale distribution of chaetognaths at Shiribeshi

379 Seamount in the northern Japan Sea; an analysis of video records of submersible remotely
380 operated vehicle. Bull. Fish. Sci. Hokkaido Univ. 55, 145-150.

381 Pearre, S.Jr, 1981. Feeding by Chaetognatha: energy balance and importance of various components
382 of the diet of *Sagitta elegans*. Mar. Ecol. Prog. Ser. 5, 45-54.

383 Perovich, D.K., 2011. The changing Arctic sea ice cover. Oceanography 24, 162-173.

384 Pierrot-Bults, A.C., 2008. A short note on the biogeographic patterns of the Chaetognatha fauna in the
385 North Atlantic. Deep-Sea Res. II 55, 137-141.

386 Pinchuk, A.I., Eisner, L.B., 2017. Spatial heterogeneity in zooplankton summer distribution in the
387 eastern Chukchi Sea in 2012-2013 as a result of large-scale interactions of water masses. Deep-
388 Sea Res. II 135, 27-39.

389 Pisareva, M.N., Pickart, R.S., Spall, M.A., Nobre, C., Torres, D.J., Moore, G.W.K., Whitledge, T.E.,
390 2015. Flow of Pacific water in the western Chukchi Sea: Results from the 2009 RUSALCA
391 expedition. Deep-Sea Res. I 105, 53-73.

392 Questel, J.M., Clarke, C., Hopcroft, R.R., 2013. Seasonal and interannual variation in the planktonic
393 communities of the northeastern Chukchi Sea during the summer and early fall. Cont. Shelf
394 Res. 67, 23-41.

395 Sameoto, D.D., 1971. Life history, ecological production, and an empirical mathematical model of the
396 population of *Sagitta elegans* in St. Margaret's Bay, Nova Scotia. J. Fish. Res. Bd. Can. 28,
397 971-985.

398 Søreide, J.E., Leu, E., Berge, J., Graeve, M., Falk-Petersen, S., 2010. Timing of blooms, algal food
399 quality and *Calanus glacialis* reproduction and growth in a changing Arctic. Global Change
400 Biol. 16, 3154–3163.

401 Terazaki, M., 1995. The role of carnivorous zooplankton, particularly chaetognaths in ocean flux. In:
402 Sakai, H., Nozaki, Y. (Eds.), Biogeochemical Processes and Ocean Flux in Western Pacific.

403 Terra Scientific Publishing Company, Tokyo, pp. 319-330.

404 Terazaki, M., 1998. Life history and distribution, seasonal variability and feeding of the pelagic
405 chaetognath *Sagitta elegans* in the subarctic Pacific: A review. *Plankton Biol. Ecol.* 45, 1-17.

406 Terazaki, M., Miller, C.B., 1986. Life history and vertical distribution of pelagic chaetognaths at Ocean
407 Station P in the subarctic Pacific. *Deep-Sea Res. A* 33, 323-337.

408 Thomson, J.M., 1947. The chaetognaths of southern Australia. *Com. Sci. Ind. Res. Bull.* 222, 1-43.

409 Tönnesson, K., Tiselius, P., 2005. Diet of the chaetognaths *Sagitta setosa* and *S. elegans* in relation to
410 prey abundance and vertical distribution. *Mar. Ecol. Prog. Ser.* 289, 177-190.

411 Walsh, J.E., 2013. Melting ice: What is happening to Arctic sea ice, and what does it mean for us?
412 *Oceanography* 26, 171–181.

413 Woodgate, R.A., Weingartner, T., Lindsay, R., 2010. The 2007 Bering Strait oceanic heat flux and
414 anomalous Arctic sea-ice retreat. *Geophys. Res. Lett.* 37, L01602, doi:10.1029/2009GL041621.

415 Zo, Z., 1973. Breeding and growth of the chaetognath *Sagitta elegans* in Bedford Basin. *Limnol.*
416 *Oceanogr.* 18, 750-756.

417

418 **Figure captions**

419 Fig. 1. Locations of sampling stations in the Chukchi Sea during 24-31 July 1991 (left) and 5-13
420 August 2007 (right). For reference, depth contours (20 and 50 m) are shown for the inset panel
421 at the lower-right corner. Open circles: stations with only *Parasagitta elegans*. Solid circles:
422 stations with both *P. elegans* and *Eukrohnia hamata*.

423 Fig. 2. Horizontal distributions of integrated mean temperature (a) and salinity (b), and the T-S
424 diagram at each station (c) in the Chukchi Sea during 24-31 July 1991 (upper) and 5-13 August
425 2007 (lower). For the T-S diagram, the data at every 10 m (0, 10, 20, 30, 40 and 50 m) are
426 connected with lines. Water masses were identified using the criteria of Danielson et al.
427 (2017). ACW: Alaskan Coastal Water, MW: melt water, BCSW: Bering-Chukchi Summer
428 Water, BCWW: Bering-Chukchi Winter Water.

429 Fig. 3. Horizontal distributions of the chaetognath *Parasagitta elegans* abundance (a) and biomass
430 (b) at each station in the Chukchi Sea during 24-31 July 1991 (upper) and 5-13 August 2007
431 (lower). Values in parentheses indicate mean abundance (ind. m⁻²) or biomass (mg DM m⁻²).

432 Fig. 4. Frequency distributions of the total lengths of the chaetognath *Parasagitta elegans* in the
433 Chukchi Sea during 24-31 July 1991 (upper) and 5-13 August 2007 (lower). For these panels,
434 the total length data are cumulative for each year. Stages (juvenile, stages I-IV) are also
435 identified. Values in parentheses indicate measured numbers (*n*). Smooth lines indicate
436 identified cohorts. Solid triangles indicate the peaks of each cohort.

437 Fig. 5. Results of the structural equation model (SEM) for the chaetognath *Parasagitta elegans*
438 abundances in the Chukchi Sea during 24-31 July 1991 (left) and 5-13 August 2007 (right).
439 The values along the pathways represent standardised path coefficient values. Arrows with
440 solid or dashed lines indicate positive or negative effects. The thickness of the arrows varies
441 with the path of the coefficient values. The overall fit of the model was evaluated using the

442 goodness-of-fit index (GFI) and the adjunct goodness-of-fit index (AGFI).

443

Table 1. Food items and feeding impact of the chaetognath *Parasagitta elegans* in the Chukchi Sea during the summers of 1991 and 2007. NPC: number of prey per chaetognath.

	Year	
	1991	2007
Food item (%)		
Copepods		
<i>Calanus</i> sp.	2.9	2.1
<i>Pseudocalanus</i> spp.	2.9	-
<i>Pseudocalanus</i> sp. C2	-	2.1
<i>Pseudocalanus</i> sp. C5F	2.9	-
<i>Pseudocalanus</i> sp. C6F	-	2.1
<i>Metridia pacifica</i> C4	2.9	-
<i>Centropages abdominalis</i>	-	2.1
<i>Eurytemora herdomani</i>	-	6.4
<i>Eurytemora herdomani</i> C6	-	2.1
Unidentified organisms	88.2	83.0
Number of individual food containing (<i>n</i>)	34	47
Number of total individual (<i>n</i>)	983	1039
Grand mean of NPC	0.035	0.045
Feeding impact (no. of prey m ⁻² day ⁻¹)	155.4	249.4
Daily percentage removal on copepods (% day ⁻¹)	1.2	0.7

Table 2. Yearly comparison in environmental parameters (integrated mean temperature and salinity), zooplankton (abundance and biomass), copepod abundance and chaetognath (*Parasagitta elegans*) abundance, biomass, mean body sizes and maturation stages in the Chukchi Sea during the summers between 1991 and 2007. For each parameter, yearly differences were tested by *U*-test. Values were means \pm SD. *: $p < 0.05$, **: $p < 0.01$, NS: not significant. Data on zooplankton and copepods are from Matsuno et al. (2011). Mean maturation stages of chaetognaths were calculated as juvenile: 1, stages I-IV: 2-5.

Parameter	Unit	Year		<i>U</i> -test
		1991	2007	
Environmental				
temperature	°C	2.9 \pm 2.0	< 5.8 \pm 2.2	**
salinity	-	31.2 \pm 0.8	< 32.1 \pm 0.5	**
Zooplankton				
abundance	10 ³ ind. m ⁻²	67.3 \pm 57.1	71.1 \pm 57.7	NS
biomass	g WM m ⁻²	37.7 \pm 26.6	42.8 \pm 60.0	NS
Copepods				
abundance	10 ³ ind. m ⁻²	13.0 \pm 13.0	< 33.7 \pm 37.2	*
Chaetognaths				
abundance	ind. m ⁻²	818.0 \pm 442.6	> 474.0 \pm 551.2	**
biomass	mg DM m ⁻²	160.8 \pm 137.2	> 78.6 \pm 97.1	**
mean body size	mm	11.5 \pm 6.2	> 9.8 \pm 5.0	**
maturation stage	-	1.5 \pm 0.8	> 1.3 \pm 0.7	**

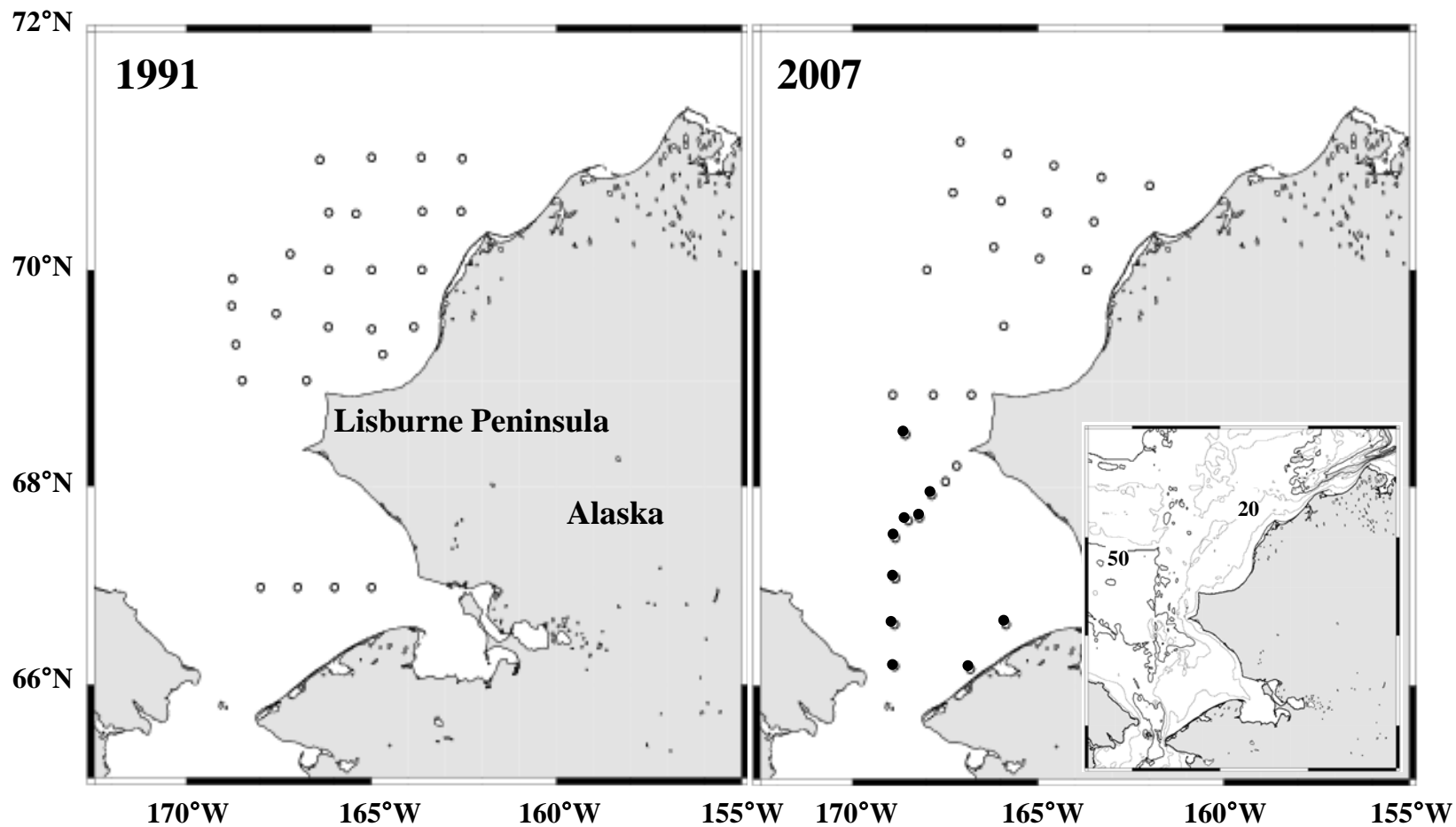


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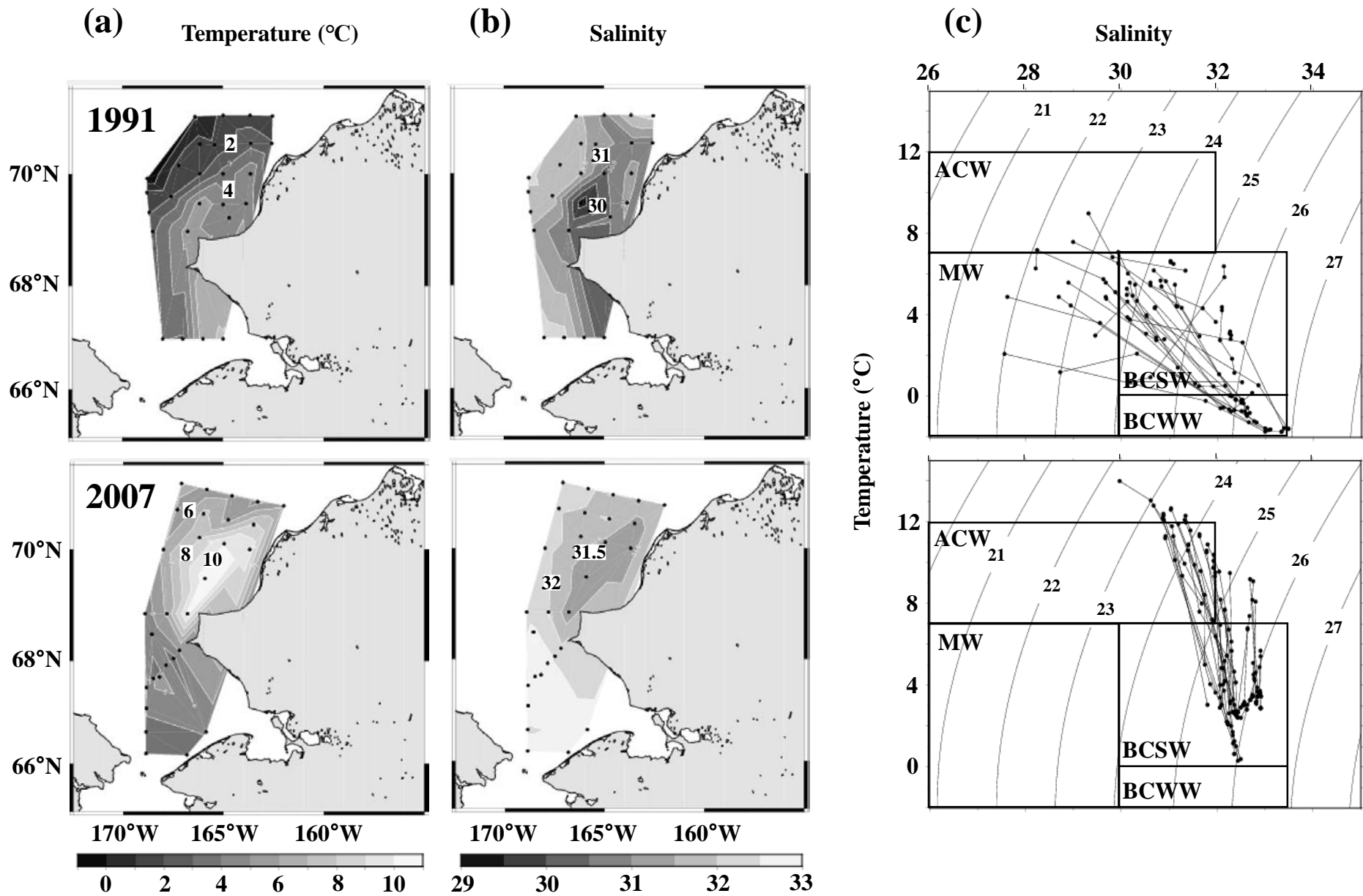


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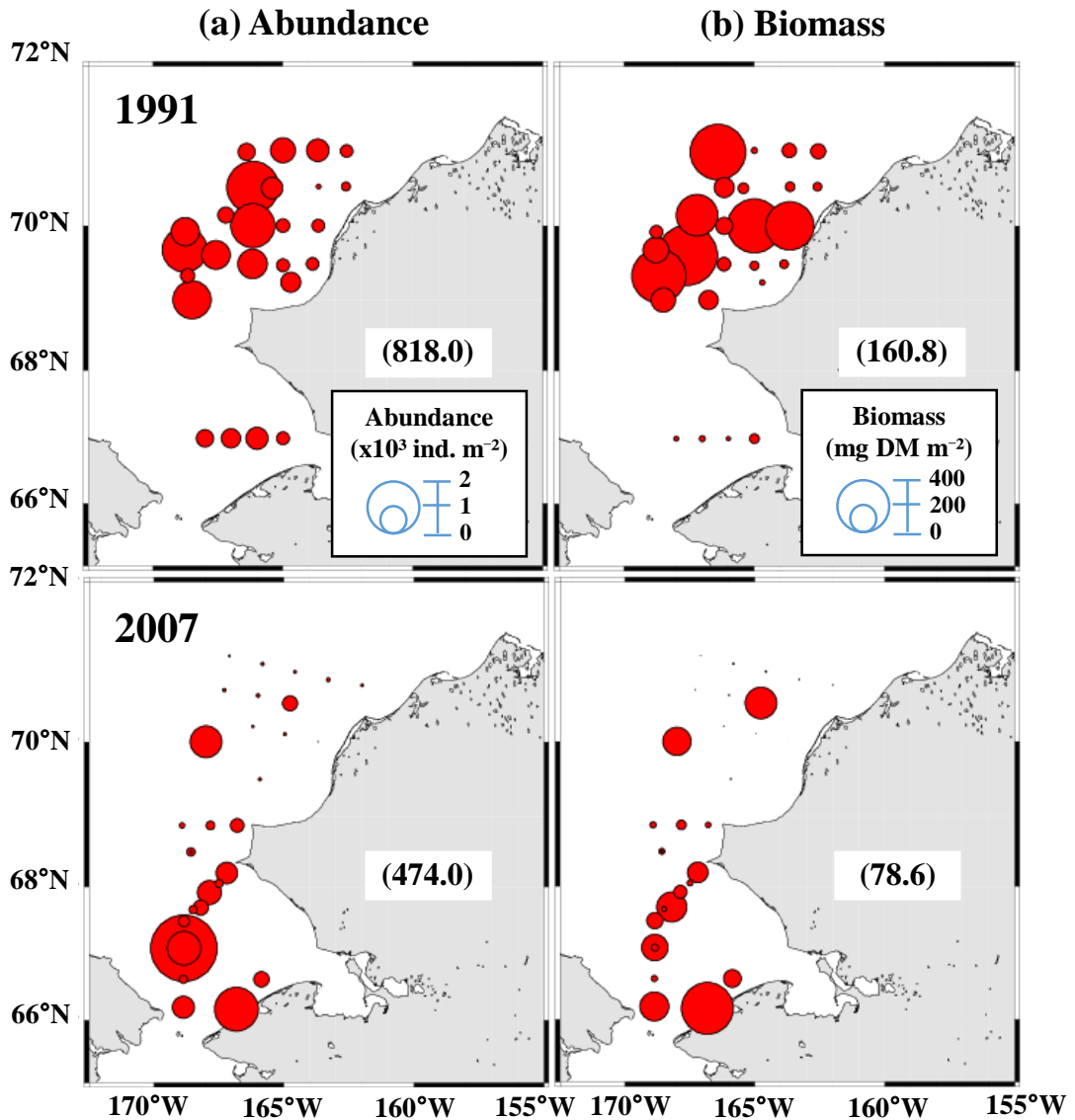


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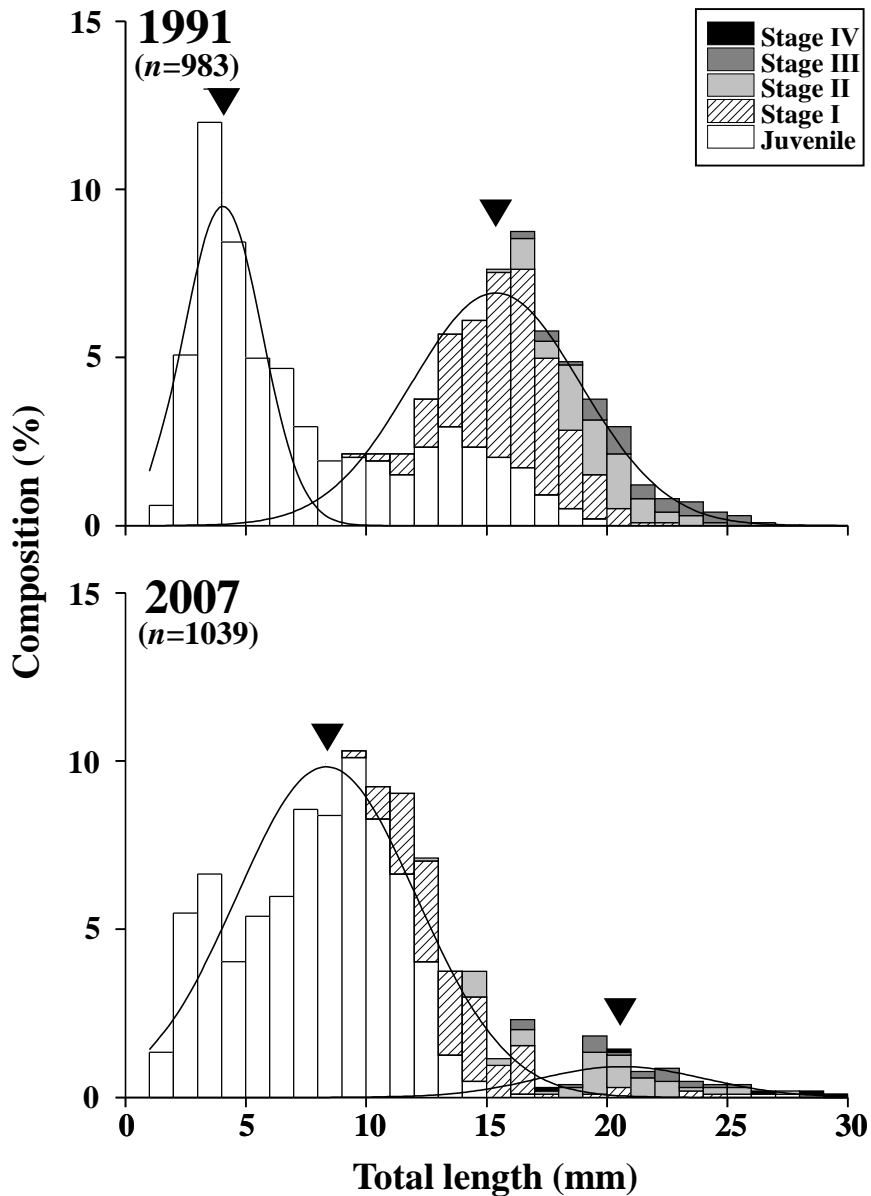


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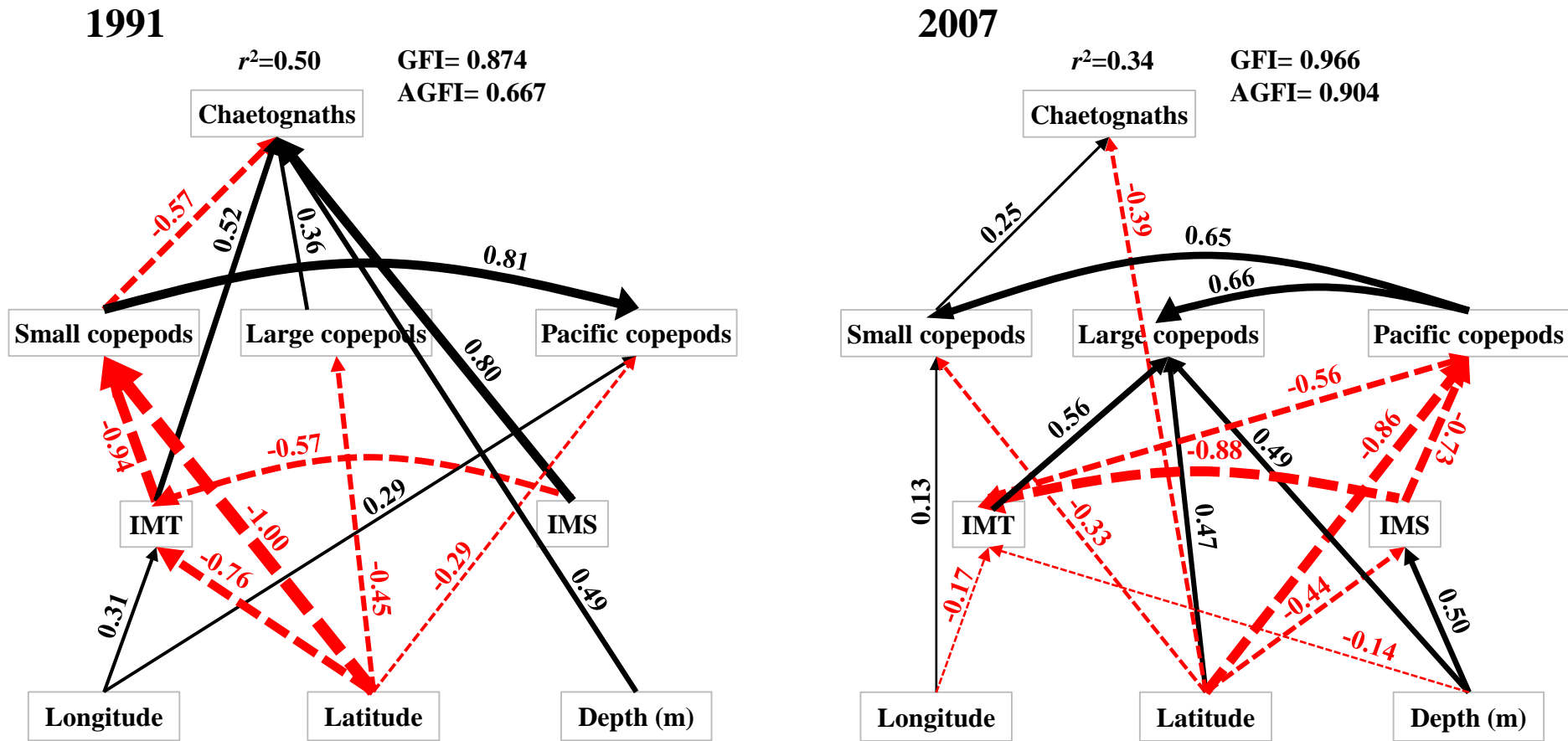


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