



Title	Abundance, horizontal and vertical distribution of epipelagic ctenophores and scyphomedusae in the northern Bering Sea in summer 2017 and 2018 : Quantification by underwater video imaging analysis
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2 Abundance, horizontal and vertical distribution of epipelagic ctenophores and scyphomedusae in the  
3 northern Bering Sea in summer 2017 and 2018: quantification by underwater video imaging analysis  
4  
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17 **Abstract**

18 We examined the abundance and horizontal and vertical distributions of epipelagic ctenophores and  
19 scyphomedusae in the northern Bering Sea using an underwater video camera during July of 2017  
20 and 2018. The effects of environmental and biological parameters on the distribution of these  
21 species were evaluated by generalized additive modelling (GAM). In 2017, the dominant  
22 ctenophore, *Bolinopsis infundibulum*, was mainly distributed in the north and west of St. Lawrence  
23 Island (SLI), and their vertical distribution varied with the region but not by the time of day. We  
24 found that *B. infundibulum* was distributed in the upper pycnocline north of SLI, but below the  
25 pycnocline west of SLI. Biological interactions with other gelatinous zooplankton may explain  
26 these regional differences in vertical distribution; GAM analysis revealed a negative interaction  
27 between *B. infundibulum* and the large scyphomedusa, *Chrysaora melanaster*, which occurred in the  
28 upper layer in the west of SLI. *B. infundibulum* may avoid that layer to reduce feeding  
29 competition. For the ctenophore, *Beroe* sp., vertical and horizontal distributions were similar to  
30 those of *B. infundibulum*, and GAM analysis also revealed a positive interaction for both species.  
31 As *B. infundibulum* is an important prey of *Beroe* sp., a prey-predator interaction may result from  
32 their similar horizontal and vertical distributions. Standing stocks of epipelagic ctenophores and  
33 scyphomedusae in 2018 were low compared to those in 2017, by a factor of 1/20 (*C. melanaster*)  
34 and 1/90 (*Beroe* sp.). This might be due to annual differences in water mass in this region, in that

35 the thermal conditions characterized by a high abundance of the dominant *B. infundibulum* in 2017  
36 (<2 and >8°C) were absent in 2018. As this drastic decrease in standing stock in 2018 was  
37 apparent for both ctenophores and scyphomedusae, food availability was hypothesized to be poor  
38 that year.

39

40 **Keywords:**

41 Ctenophores, Scyphomedusae, Northern Bering Sea, Vertical distribution, Horizontal distribution,

42 Imaging analysis

43

44

45 **1. Introduction**

46           Recently, increases in the abundance of large ctenophores and scyphomedusae have been  
47 reported in various oceans worldwide, likely due to human alteration of marine environments and  
48 climate change (Purcell et al., 2007; Condon et al., 2013; Duarte et al., 2013). The main food  
49 sources of ctenophores and scyphomedusae in higher latitudes are mesozooplankton, especially  
50 copepods (Brodeur et al., 2002; Purcell et al., 2010). Ctenophores and scyphomedusae are thus  
51 competitors of the planktivorous fishes, and also act as predators upon larval fishes; thus, the  
52 abundance of large gelatinous zooplankton can have a great effect on fish stocks (Brodeur et al.,  
53 2002; Purcell et al., 2007; Robinson et al., 2014). As large gelatinous zooplankton are composed  
54 mainly of water and require less organic material for their body composition, they can respond to  
55 environmental changes more rapidly than crustacean zooplankton, and their biomass can vary  
56 dramatically between years (Falkenhaus, 1996; Brodeur et al., 2008).

57           The northern Bering Sea, the target area of the present study, is a transit region for the  
58 warmer waters of southern origin (Alaskan Coastal Water, Bering Shelf Water, Anadyr Water),  
59 which intrude into the western Arctic Ocean (Shimada et al., 2006; Sasaki et al., 2016; Danielson et  
60 al., 2017). A polynya forms south of St. Lawrence Island (SLI), the largest island in this region,  
61 and is characterized as being ice-free, even in winter (Grebmeier and Cooper, 1995). Recently, a  
62 drastic decrease in the ice-covered area and an early ice retreat in the northern Bering Sea has been

63 reported (Comiso et al., 2008; Parkinson and Comiso, 2013; Stabeno and Bell, 2019).  
64 Additionally, changes in zooplankton biomass, a northern shift of the fish community, and a mass  
65 mortality of seabirds occurred during the winter of 2017/2018 and spring/summer of 2018  
66 (Cornwall, 2019; Duffy-Anderson et al., 2019; Huntington et al., 2020). Under conditions of  
67 greater variability in the environment and marine ecosystem, the amount and distribution of  
68 ctenophores and scyphomedusae were also expected to change. However, ecological information on  
69 these species is presently scarce for this region.

70           The methods used to quantify ctenophores and scyphomedusae have several limitations  
71 (Graham et al., 2003, Uye et al., 2017). Traditional sampling using a plankton net tow is hampered  
72 by patchy spatio-temporal distributions, relatively large body size, low abundance, and net  
73 avoidance, leading to inevitable underestimation of their biomass and species diversity (Youngbluth  
74 and Båmstedt, 2001; Graham et al., 2003; Raskoff et al., 2005; Uye et al., 2017). The fragile  
75 bodies of ctenophores and scyphomedusae are also heavily damaged by net towing (Graham et al.,  
76 2003; Raskoff et al., 2005; Uye et al., 2017). Large-volume trawl nets have been used; however,  
77 using these nets requires large effort and cost compared to plankton sampling. Moreover, changes  
78 in the mouth area and collection efficiency varies with mesh size and towing speed. These nets  
79 cause serious damage to the fragile bodies of gelatinous zooplankton, making quantitative collection  
80 difficult for ctenophores and scyphomedusae (Graham et al., 2003, Uye et al., 2017). To overcome

81 these problems in the quantification of ctenophores and scyphomedusae, alternative non-capture  
82 methods such as sonar cameras (Han and Uye, 2009), video cameras using a Remotely Operated  
83 Vehicle (Båmstedt and Martinussen, 2015), and visual monitoring using ships and airplanes (Purcell  
84 et al., 2000) have been used.

85           In the Bering Sea, Brodeur et al. (2017) reported horizontal distributions, and seasonal and  
86 annual changes in ctenophores and scyphomedusae based on data collected by trawl nets, although  
87 there was the paucity of data for the northern Bering Sea. The vertical distributions of ctenophores  
88 and scyphomedusae in the southeastern Bering Sea have been observed using a video camera  
89 mounted on an ROV (Brodeur, 1998; Brodeur et al., 2002). Annual variations in the biomass of the  
90 large scyphomedusa, *Chrysaora melanaster*, over the southeastern Bering Sea shelf has previously  
91 been analysed using Generalized Additive Models (GAM) to explore which environmental variables  
92 might explain the variability (Brodeur et al., 2008). Although the northern Bering Sea is  
93 characterized by large interannual changes in the ice-covered area and timing of the ice retreat, few  
94 studies have investigated interannual changes in ctenophores and scyphomedusae in this region.

95           In the present study, we quantified the horizontal and vertical distributions, and annual  
96 changes in the abundances of ctenophores and scyphomedusae using an underwater video camera in  
97 the northern Bering Sea during the summers of 2017 and 2018. Interactions among vertical,  
98 horizontal, and annual changes in the abundance of ctenophores and scyphomedusae were assessed

99 with environmental parameters (depth, temperature, salinity, diel period, year, and location relative  
100 to the pycnocline) and biological parameters (mesozooplankton biomass, other species of  
101 ctenophores and scyphomedusae) by GAM analysis.

102

## 103 **2. Material and methods**

### 104 *2.1. Field observation*

105 Imaging data for ctenophores and scyphomedusae were collected by vertical casts of a frame camera  
106 at 21 (2017) and 14 (2018) stations located between 63°00'–66°44'N and 166°30'–174°50'W in the  
107 northern Bering Sea. These sampling stations were occupied by the T/S *Oshoro-Maru* during 9–22  
108 July 2017 and 2–12 July 2018 (Fig. 1). Imaging data down to 50 m were collected by dead-slow  
109 (0.1 m s<sup>-1</sup>) vertical deployment of an underwater video camera (Marine Arkas, Kowa Co. Ltd.)  
110 mounted within a stainless frame of 1.0 × 1.0 m bottom and 1.5 m depth (Fig. 2B). A charge-  
111 coupled device (CCD) camera (NTSC PA-290) was equipped with a *f*2.9 lens that had 0.035 lux  
112 light sensitivity. The final resolution of each digital frame was 768 (horizontal) by 494 (vertical)  
113 pixels. The *in situ* images were monitored from the ship. To evaluate diel changes in vertical  
114 distribution, observations were made at 1 h intervals at one station (St. 10) during 19:40–7:10, 13–14  
115 July 2017 (total number of samples = 11) (Appendix A). Observations were made both day and  
116 night at three additional stations (St. 14, 20, and 23) in 2017. At each station, temperature and



117 salinity were measured using a Conductivity Temperature Depth (CTD) sensor (SBE911, Sea-Bird  
118 Electronics, Inc.). To evaluate mesozooplankton biomass, a vertically-stratified tow of a 60 cm  
119 opening-closing net (mesh size: 100  $\mu$ m) (Kawamura, 1989) was conducted from the sea-surface to  
120 the thermocline, and from the thermocline to near-bottom. Mesozooplankton samples were  
121 preserved in 5% (v/v) borax-buffered formalin seawater.

122           The underwater camera (Marine Arkas, Kowa Co. Ltd.) was equipped with two halogen  
123 lights (JCD100V-150W) with 150W and 3300 lumen luminous flux and a pressure-depth sensor  
124 (model P193-010-45, SENSIT., Co. Ltd., Hampshire, UK) with a precision of  $\pm 0.25\%$ FS. A  
125 picture of the frame camera is presented in Fig. 2B. Using the bottom observation frame as a  
126 guide, the camera was able to image an observational area of  $1.2 \times 0.8$  m (Fig. 2B, C). On the side  
127 of the frame, a current fin ( $0.8 \times 0.3$  m) was attached so that the horizontal current was flowing in  
128 one direction along the diagonal of the bottom observation frame. Sinkers (20 kg each) were set at  
129 the four corners of the frame. We measured the wire angle, and, because of the heavy weight of the  
130 camera and frame, the angles were less than  $5^\circ$  at each cast. Underwater videos were transferred  
131 on-board through a tether cable and recorded using an HDD and DVD recorder (Toshiba RD-X4).  
132 The recording method was MPEG2. The depth data were displayed on a captured image and were  
133 recorded using video imaging data. For examples of the video images, see video supplemental  
134 materials captured for Cast 14 at St. 10 on 14 July 2014 (Video 1) and for Cast 27 at St. 19 on 19

135 July 2017.

136

137 *2.2. Quantification of ctenophores and scyphomedusae*

138 In the laboratory on land, all ctenophores and scyphomedusae within the observation frame (0.8 m x

139 1.2 m) were identified and counted in 2 m vertical intervals from the recorded video. As the frame

140 camera was towed at a speed of 0.1 m s<sup>-1</sup>, video images obtained at 2 m depth intervals corresponded

141 to 20 s (= 2.0/0.1). Depth data were expressed with 0.1 m accuracy, and the error for estimated

142 depths obtained by the sonar- equipped ship was less than 0.5 m. To evaluate the flow rates of

143 horizontal currents, the diagonal passage time ( $Pt$ , s) of ctenophores, scyphomedusae and marine

144 snow within the observation field was measured at 10 m intervals. The  $Pt$  was not varied with the

145 targets. For real images of the video, see video supplemental materials. Note that we measured

146 current speed every 10 m constantly and applied these current data for jellyfishes quantified with 2

147 m interval.

148 To calculate individual density, observation volume over 2 m intervals ( $V$ , m<sup>3</sup>) was

149 calculated from the following equation (Fig. 2C):

150 
$$V = 2 \times 1.2 \times 0.8 \times 20 \times 1/Pt,$$

151 where,  $2 \times 1.2 \times 0.8$  is the volume of the observation field (height × width × depth, m<sup>3</sup>). Thus,  $1/Pt$

152 represents the changes in viewing within 1 s. As a 2 m vertical movement of the video camera

153 required 20 s., “ $20 \times 1/Pt$ ” represents the change in view caused by horizontal advection within a 2  
154 m observation distance. Swimming speeds of ctenophores and scyphomedusae may also affect  
155 their quantification. The swimming speed ( $V$ :  $\text{cm s}^{-1}$ ) of ctenophores is known to be a function of  
156 diameter ( $Dia$ : cm):  $V = 0.12 + 0.04 Dia$  (Cowan and Houde, 1992). If we assume 15-20 cm  
157 diameter, the swimming speed of the ctenophore would have been 0.72-0.92  $\text{cm s}^{-1}$ . From  $Pt$ , the  
158 horizontal current speed was calculated to be ca. 0.5-2.0  $\text{m s}^{-1}$ . Thus, since horizontal current speed  
159 was generally faster than the swimming speed of ctenophores and scyphomedusae, the effect of their  
160 swimming speeds on the quantification of their numbers was ignored.

161 Ctenophores and scyphomedusae were quantified for both the descent ( $D$ ) and ascent ( $A$ )  
162 of the tows, and the data from both directions corresponded well ( $D = 0.857 \times A$ ,  $r^2 = 0.742$ ,  $p$   
163  $< 0.0001$ ,  $n = 561$ ) (Appendix B). Thus, we calculated the mean descent and ascent abundance for  
164 each depth. The settling volume for mesozooplankton samples collected by the closing net was  
165 measured with 0.1 mL accuracy and expressed as their biovolume biomass ( $\text{mL m}^{-3}$ ).

166

### 167 2.3. Statistical analysis

168 To examine diel changes in vertical distribution, the abundances at depths of 10, 25, 50, 75, and 90%  
169 ( $D_{10\%}$ ,  $D_{25\%}$ ,  $D_{50\%}$ ,  $D_{75\%}$ , and  $D_{90\%}$  respectively, Pennak, 1943) were calculated for all stations at  
170 which day-night observations were made (St. 10, 14, 20, 23, in 2017). To evaluate diel vertical

171 migration,  $D_{50\%}$  was compared between the day ( $n=7$ ) and night ( $n=4$ ) using a Mann Whitney U-test  
172 at St. 10. For the remaining stations (St. 14, 20, 23) where day and night sampling was conducted,  
173 the Kolmogorov-Smirnov test was used to evaluate diel changes in vertical distribution (Sokal and  
174 Rohlf, 1995).

175 The effects of environmental and biological parameters on the distribution of ctenophores  
176 and scyphomedusae were analysed by GAM. The densities of ctenophores and scyphomedusae  
177 were applied as response variables, and environmental and biological parameters, such as  
178 hydrography (temperature, salinity), depth, day-night, year, upper/lower pycnocline,  
179 mesozooplankton biomass, and the densities of other ctenophores and scyphomedusae were applied  
180 as explanatory variables. The pycnocline was defined as the depth at which the seawater density  
181 was higher than that at the 5 m depth by  $0.1 \text{ kg m}^{-3}$  (Danielson et al., 2011). For the GAM analysis,  
182 R software with “mgcv” package was used (Wood, 2017).

183

### 184 **3. Results**

#### 185 *3.1. Hydrography*

186 Cross-sectional distributions of temperature and salinity along each line transect in the northern  
187 Bering Sea during 2017 and 2018 are shown in Figs. 3 and 4, respectively. In 2017, water  
188 temperatures ranged from  $-1.26$  to  $11.6^{\circ}\text{C}$  and salinities from 30.2 to 32.9 psu, respectively (Fig. 3).

189 In most locations, the upper layer was characterized by warm temperatures and low salinity. No  
190 pycnocline developed north of 66°N, near the Bering Strait, whereas a pycnocline was observed  
191 around 6–32 m in the western and southern regions of SLI, with substantial differences in  
192 temperature between the upper and lower layers. Conversely, in 2018, temperature and salinity  
193 ranged from -0.21 to 12.8°C and from 28.3 to 32.9 psu, respectively (Fig. 4). Pycnocline  
194 development was much weaker in 2018 than in 2017. The differences in temperature between the  
195 upper and lower layers of the pycnocline were smaller in 2018 compared with 2017.

196

### 197 3.2. Horizontal distribution of ctenophores and scyphomedusae

198 Horizontal distributions of ctenophore and scyphomedusa standing stocks (ind. m<sup>-2</sup>) at each  
199 sampling station in 2017 and 2018 are shown in Fig. 5. Three taxa of large gelatinous zooplankton  
200 were commonly observed: the ctenophores, *Bolinopsis infundibulum* and *Beroe* sp., and the  
201 scyphomedusae, *Chrysaora melanaster* (Fig. 2A). Among these, *B. infundibulum* was the most  
202 numerous species in both 2017 and 2018. In 2017, the standing stock of *B. infundibulum* was 0–  
203 35.6 ind. m<sup>-2</sup> and was the greatest north and west of SLI. The maximum abundance of *C.*  
204 *melanaster* and *Beroe* sp. occurred at 0.689 and 0.567 ind. m<sup>-2</sup>, respectively, and they were abundant  
205 west and south of SLI, and north of SLI to the Bering Strait, respectively. In 2018, standing stocks  
206 of all species were much lower than those in 2017, and their mean abundance in 2018 was 1/90 (*C.*

207 *melanaster*)–1/20 (*Beroe* sp.) of those in 2017 (Fig. 5).

208

209 3.3. Diel changes in the vertical distribution of *Bolinopsis infundibulum*

210 Diel changes in the vertical distribution of *B. infundibulum* were examined at four stations in 2017

211 (Fig. 6). At St. 10, where multiple observations were made, day and night  $D_{50\%}$  (mean  $\pm$  1 sd) was

212  $6.97 \pm 4.62$  and  $1.92 \pm 0.32$  m, respectively. Although the night  $D_{50\%}$  was 5 m shallower than the

213 day  $D_{50\%}$ , this difference was not significant ( $p > 0.05$ , *U*-test), suggesting that there was no diel

214 vertical migration (DVM). For the three stations with only one day-night observation (St. 14, 20,

215 23), diel differences were detected at St. 14 and 20 (St. 14:  $p < 0.005$ , St. 20:  $p < 0.001$ ,

216 Kolmogorov-Smirnov test); however, the diel pattern varied with the station. A nocturnal ascent

217 occurred at St. 14, while a nocturnal descent occurred at St. 20. The diel changes in  $D_{50\%}$  were 5.3

218 m (St. 14) and 5.5 m (St. 20). No significant change was detected between the day and night

219 vertical distributions at St. 23 ( $p > 0.05$ ), likely due to the extremely low abundance at that station

220 (Appendix D). For details of each observation, see Appendix C (St. 10) and Appendix D (Sts. 14,

221 20, 23).

222

223 3.4. Vertical distributions of ctenophores and scyphomedusae

224 In 2017, the vertical distribution of *B. infundibulum* showed a clear regional pattern (Fig. 7). This

225 species was distributed throughout the water column north of the Bering Strait (St. 1, 5), but was  
226 distributed around or below the pycnocline south of the Bering Strait (St. 7, 9). *B. infundibulum*  
227 was primarily distributed at shallower depths than the pycnocline north of SLI (St. 12, 13), while a  
228 bimodal distribution with peaks in the upper and lower layers of the water column was observed  
229 northwest of SLI (St. 16, 18). West of SLI (St. 19, 20, 24), this species was distributed below the  
230 pycnocline.

231 In 2017, *C. melanaster* was distributed in a layer shallower than the pycnocline (Fig. 8).

232 In the region west and south of SLI, *C. melanaster* was distributed at shallower depths than the  
233 pycnocline with a maximum density at 0.161 ind. m<sup>-3</sup> (St. 22, 6–8 m) for these regions.

234 *Beroe* sp. were distributed at depths shallower than the pycnocline south of the Bering  
235 Strait (St. 6, 9), and both above and below the pycnocline north of SLI (St. 13, 14) (Fig. 9).  
236 Conversely, they were distributed entirely below the pycnocline west and south of SLI (St. 18, 20,  
237 22, 24).

238

### 239 3.5. Interannual changes in ctenophores and scyphomedusae densities

240 Based on data from all sampling stations, the densities of the most dominant ctenophore (*B.*  
241 *infundibulum*) in 2017 and 2018 are shown with the hydrography in Fig. 10. Annual changes were  
242 observed between 2017 and 2018, where 2017 showed a bimodal distribution, with high abundances

243 at >8 and <2°C, and low abundance at intermediate temperatures (2–8°C). Conversely, the thermal  
244 range available in 2018 was mostly limited to 2–8°C and *B. infundibulum* showed very low densities  
245 within these temperature ranges.

246

### 247 3.6. GAM Environmental Relationships

248 In 2018, depth, temperature, salinity, and zooplankton all had significant effects on *B. infundibulum*,  
249 which were abundant at night and below the pycnocline; these factors were negatively related to *C.*  
250 *melanaster* abundance, and positively related to *Beroe* sp. (Table 1). There was a significant  
251 positive relationship between *C. melanaster* abundance and temperature, salinity, and zooplankton  
252 biomass, and a negative relationship with *B. infundibulum* abundance. There was a significant  
253 relationship between *Beroe* sp. abundance and depth, temperature, salinity, and zooplankton  
254 biomass, and a positive interaction with *B. infundibulum* abundance. Smoothing spline regressions  
255 between ctenophore and scyphomedusae abundance and environmental parameters with a significant  
256 relationship are shown in Fig. 11. The abundance of *B. infundibulum* was high at depths <24 m,  
257 temperatures of -1–2, 5.5–7.5, and 9–10°C, salinities of >30.7, 31.8–32.1, and >32.3 psu, and  
258 zooplankton biomasses of 0.1–0.6, 1.4–3.0, and 3.4–4.1 mL m<sup>-3</sup>. The abundance of *C. melanaster*  
259 was high at temperatures >5.5°C, salinities between 31.0 and 32.4 psu, and zooplankton biomasses  
260 of <1.7, and 3.0–4.4 mL m<sup>-3</sup>. The abundance of *Beroe* sp. was high at depths <14 m, temperatures



261 <6.9°C, salinities of <30.4, 30.8–31.3, and 31.7–32.8 psu, and zooplankton biomasses between 0.2–  
262 2.1 mL m<sup>-3</sup>.

263

## 264 **4. Discussion**

### 265 *4.1. Quantification of ctenophores and scyphomedusae*

266 In the present study, we used an underwater video camera to collect quantitative data on ctenophores  
267 and scyphomedusae during day and night, even under dark conditions in the deepest layers using  
268 artificial light (3300-lumen luminous flux). Use of an underwater video camera to quantify  
269 ctenophores and scyphomedusae has been somewhat limited in past studies by reduced visibility and  
270 difficulty quantifying their abundance in high turbidity waters (Honda and Watanabe, 2007; Honda  
271 et al., 2016), but we did not encounter high turbidity water in our study region in either year as  
272 judged by using the square frame at the bottom of the frame as a guide.

273 Several metrics have been presented to quantify data on ctenophores and scyphomedusae  
274 obtained with an underwater video camera. These include individual number over each observation  
275 time within a certain depth range (ind. min<sup>-1</sup> or ind. hour<sup>-1</sup>) (Toyokawa et al., 2003; Raskoff et al.,  
276 2005; Honda and Watanabe, 2007; Raskoff et al., 2010), the individual number observed at each  
277 depth (number observed) (Purcell et al., 2010; Båmstedt and Martinussen, 2015), and species  
278 composition within the total observed number throughout the water column (%) (Brodeur, 1998).

279 In the present study, we calculated the observed volume by multiplying the observation area ( $1.2 \times$   
280  $0.8$  m) by depth ( $2$  m) and considered the change in view caused by horizontal advection within a  $2$   
281 m observation (Fig. 2C). A similar calculation method has been used in previous studies.  
282 Youngbluth and Båmstedt (2001) calculated volume by multiplying the observation area by vertical  
283 depth. To account for horizontal advection, the current flow of the water mass was applied (Nogata  
284 et al., 2009), and by measuring the horizontal current using a shipboard acoustic Doppler current  
285 profiler (ADCP), Honda et al. (2016) were able to calculate volumes considering horizontal  
286 advection. On our cruises, horizontal current was also measured by the shipboard ADCP.  
287 However, vertical changes in the horizontal current speed were also observed in the present study.  
288 Thus, we measured horizontal current speed at depth using the time taken for a particle (e.g. marine  
289 snow) to pass through the observation frame at  $10$  m depth intervals. As we set the current fin for  
290 the frame, the horizontal current was flowing diagonally; thus, it was possible to quantify the  
291 horizontal current measurements in this study.

292 Båmstedt and Martinussen (2015) reported a maximum density of *B. infundibulum* of  $2\text{--}5$   
293 ind.  $\text{m}^{-3}$  at  $0\text{--}50$  m depths in a western Norwegian fjord. This value corresponds well with the  
294 maximum density ( $3.58$  ind.  $\text{m}^{-3}$ ) observed in our study. For *C. melanaster*, a maximum density of  
295  $0.07$  ind.  $\text{m}^{-3}$  has been reported for the southeastern Bering Sea shelf (Brodeur, 1998), whereas in the  
296 present study, we observed  $0.16$  ind.  $\text{m}^{-3}$ . Thus, our use of underwater video to quantify individual

297 density, considering horizontal advection, seems appropriate and comparable to the results of  
298 previous studies.

299

#### 300 4.2. Diel vertical migration of ctenophores and scyphomedusae

301 For *B. infundibulum*, no diel changes in vertical distribution were observed at two stations (St. 10,  
302 23), nocturnal ascent was observed at one station (St. 14), and nocturnal descent was found at one  
303 station (St. 20). However, where changes were observed, the diel differences were small (5.3–5.5  
304 m). Little information is available regarding the DVM of ctenophores (Vereshchaka, 2002;  
305 Haraldsson et al., 2014; Júnior et al., 2015). The absence of DVM in ctenophores has been  
306 attributed to their lacking organs that can detect light (Graham et al., 2001). However, it was  
307 recently reported that ctenophores may possess an organ capable of detecting light (Haraldsson et al.,  
308 2014).

309 The DVM pattern observed for *B. infundibulum* varied with the station, and the magnitude  
310 (5.3–5.5 m) was close to the sampling interval of this study (2 m), and relatively small compared to  
311 the entire observational depth (50 m). Therefore, we conclude that *B. infundibulum* did not perform  
312 extensive DVM in our study region. The DVM of *Beroe* spp. has been reported for the northeast  
313 Atlantic and the south Brazilian Bight (Roe et al., 1984; Júnior et al., 2015), but in the present study,  
314 because of the low abundance, DVM could not be evaluated for *Beroe* sp. Several studies have

315 reported the DVM of scyphomedusae (Youngbluth and Båmstedt, 2001; Graham et al., 2001;  
316 Gorbatenko et al., 2009; Brodeur et al., 2017). For *C. melanaster*, no DVM had been reported in  
317 the southwestern Bering Sea shelf region (Brodeur et al., 2017), and in the present study, *C.*  
318 *melanaster* was distributed above the pycnocline during both day and night.

319

### 320 4.3. Horizontal and vertical distribution of ctenophores and scyphomedusae

#### 321 4.3.1. *Bolinopsis infundibulum*

322 The vertical distribution of *B. infundibulum* varied with the region and was distributed above the  
323 pycnocline north of SLI, and below the pycnocline west of SLI. The region west of SLI was  
324 characterized by an extremely cold water mass ( $<0^{\circ}\text{C}$ ) below the pycnocline (Fig. 3), and the  
325 occurrence of *C. melanaster* above the pycnocline (Fig. 8). Therefore, the deep distribution of *B.*  
326 *infundibulum* in the west of SLI could have been caused by both physical oceanographic factors and  
327 biological interaction factors. We were unable to assess the relative contributions of these variables.

328 A polynya was present in 2017 (Grebmeier, J.M. pers. comm.), and the loss of saline and  
329 dense brine water during the formation of ice may have forced *B. infundibulum* to be distributed  
330 below the pycnocline. Several ctenophores, *Mnemiopsis leidyi*, *Pleurobrachia* spp., and *Beroe*  
331 spp., do not appear to cross a strong pycnocline, and instead distribute either above or below the  
332 pycnocline (Roe et al., 1984; Vereshchaka, 2002; Haraldsson et al., 2014). When a strong

333 pycnocline developed west of SLI, *B. infundibulum* was restricted to below the pycnocline and did  
334 not appear to migrate upward across the pycnocline. *B. infundibulum* can live under cold (<0°C)  
335 conditions (Raskoff et al., 2005), and may be able to survive under the cold conditions that occur  
336 below the pycnocline in this region.

337           Due to predator-prey interactions, the occurrence of large scyphomedusae *C. melanaster*  
338 above the pycnocline west of SLI may have caused *B. infundibulum* to avoid that layer. GAM  
339 analysis revealed a negative interaction between these two species. *C. melanaster* feeds on  
340 gelatinous zooplankton (Purcell, 1991), and a prey-predator interaction between *C. melanaster* and  
341 *Bolinopsis* spp. has been noted off Japan (Kinoshita et al., 2006); thus, the distribution of *B.*  
342 *infundibulum* that we observed may have been a behavioural avoidance of predation by *C.*  
343 *melanaster*. Indeed, in the Nordic fjord, *B. infundibulum* has been shown to remain below the  
344 pycnocline to avoid predation from a large predatory scyphomedusae, *Cyanea capillata* (Båmstedt  
345 and Martinussen, 2015). However, in the Canada Basin, in the western Arctic Ocean, the  
346 coexistence of *C. melanaster* and *B. infundibulum* within the same depth layer has been reported  
347 (Raskoff et al., 2005; Purcell et al., 2010).

348           Although we identified two possible factors that may explain horizontal changes in the  
349 vertical distribution of *B. infundibulum*, physical oceanographic factors and biological interaction  
350 factors, we cannot conclude which factor is most important in determining the regional changes in

351 vertical distribution. *B. infundibulum* has been reported to occur at depths up to 1250 m in the  
352 Oyashio Current in the western subarctic Pacific Ocean (Toyokawa et al., 2003) and Canada Basin,  
353 in the western Arctic Ocean (Raskoff et al., 2005; Purcell et al., 2010). These findings suggest that  
354 *B. infundibulum* exhibits much flexibility in terms of their vertical distribution and ability to adapt to  
355 various environments and regions.

356

#### 357 4.3.2. *Chrysaora melanaster* and *Beroe* sp.

358 We found that *C. melanaster* was distributed above the pycnocline at most stations, and the GAM  
359 analysis revealed a significant positive interaction between *C. melanaster* abundance and  
360 temperature ( $p < 0.01$ , Table 1, Fig. 11). Previous studies have reported that *C. melanaster* is  
361 distributed above the pycnocline (Brodeur, 1998; Brodeur et al., 2002; Raskoff et al., 2005;  
362 Gorbatenko et al., 2009; Radchenko, 2013; Brodeur et al., 2017). Raskoff et al. (2005) reported  
363 that the above pycnocline distribution of *C. melanaster* may be explained by their feeding on  
364 copepods and gelatinous zooplankton, which are more abundant above the pycnocline. Radchenko  
365 (2013) noted that the standing stock of zooplankton is more important than the thermal condition  
366 above the pycnocline in explaining the vertical distribution of this species. Previous studies have  
367 shown that *C. melanaster* feed on crustaceans, gelatinous zooplankton, larvae of walleye pollock,  
368 ostracods, and decapod larvae in the Bering Sea (Brodeur et al., 2002; Zavolokin et al., 2008;

369 Ruzicka et al., 2020). Video images from the present study showed that hydromedusae *Aglantha*  
370 *digitale* was abundant above the pycnocline (Maekakuchi unpublished data). Since *A. digitale* is  
371 also an important food item for *C. melanaster* (Radchenko, 2013), we suggest that the observed  
372 distribution of *C. melanaster* may be related to the abundance of their food items, such as copepods  
373 and gelatinous zooplankton, above the pycnocline.

374 Standing stocks of *C. melanaster* were highest in the southern region in this study (south  
375 of SLI). *C. melanaster* is very abundant in the southeastern Bering Sea shelf where it can exert a  
376 substantial effect on other pelagic animals and marine food web structure in that region (Brodeur et  
377 al., 2002, 2008), and *C. melanaster* has been reported in lower abundances farther north, in the  
378 Canada Basin of the western Arctic Ocean (Raskoff et al., 2005; Purcell et al., 2010). These  
379 observations suggest that the high standing stocks of *C. melanaster* in the southern region of this  
380 study may reflect the regional differences in standing stocks.

381 The GAM analysis revealed a positive relationship between *Beroe* sp. and the abundance  
382 of *B. infundibulum*. *Beroe* sp. were mainly distributed above the pycnocline, but they were  
383 distributed below the pycnocline in the west of SLI, which parallels the regional pattern of vertical  
384 distribution for *B. infundibulum* (Fig. 9). We suggest that predator-prey relationships may be the  
385 cause of this parallel regional vertical distribution pattern of *Beroe* sp. with those of *B. infundibulum*.  
386 *Beroe* spp. has been shown to feed on *B. infundibulum* (Greve, 1970; Purcell, 1991), and the vertical

387 distribution of *Beroe cucumis* has been documented to be similar to that of their prey (Falkenhaus,  
388 1996; Bandara et al., 2016). However, as noted for *B. infundibulum*, *Beroe* sp. may be restricted in  
389 their distribution to below the pycnocline due to highly saline water, so there could also be a  
390 physical oceanographic mechanism affecting their distribution.

391

#### 392 4.4. Interannual changes in ctenophores and scyphomedusae

393 This study was conducted in the same location and season over two consecutive years and standing  
394 stocks of ctenophores and scyphomedusae were much lower in 2018 than in 2017, by a factor of  
395 1/20 to 1/90. The biomass of large scyphomedusae in the southeastern Bering Sea has been shown  
396 to fluctuate annually due to climate variability (Brodeur et al., 2017). There, the biomass of large  
397 scyphomedusae, which is dominated by *C. melanaster*, increased 20-fold from 1975 to 2000, then  
398 decreased to one-third of the maximum after 2001, possibly due to climate-induced changes in the  
399 lower trophic levels (Brodeur et al., 2008). In warm years, ice melts quickly, leading to late  
400 pycnocline development and phytoplankton bloom initiation; thus, smaller copepods such as  
401 *Pseudocalanus* and *Acartia* dominate the zooplankton biomass (Hunt et al., 2011), which may result  
402 in poor food conditions for *C. melanaster* (Brodeur et al., 2008). Conversely, in cold years, the  
403 phytoplankton bloom initiates earlier, and large copepods, such as *Calanus*, dominate the  
404 zooplankton biomass and these provide sufficient food conditions for the survival and growth of



405 ephyrae of *C. melanaster*, thus leading to an increase in scyphomedusae biomass (Brodeur et al.,  
406 2008). Large changes in biomass over a short period have been observed in other regions. For  
407 example, the biomass of ctenophores and scyphomedusae along the Kurile Islands in the Western  
408 Pacific Ocean increased 10-fold from 2011 to 2012; intrusions from the Bering Sea and Okhotsk Sea  
409 was invoked to explain this high biomass (Radchenko, 2013). Thus, there are large annual  
410 fluctuations in the biomass of ctenophores and scyphomedusae, which are related to climate change  
411 and oceanographic conditions.

412 Observations of water masses with high ( $>8^{\circ}\text{C}$ ) and low ( $<2^{\circ}\text{C}$ ) temperature conditions  
413 that were characterized by a high abundance of *B. infundibulum* in 2017 were much more limited in  
414 2018, and a decrease in optimal thermal conditions for *B. infundibulum* ( $>8$  and  $<2^{\circ}\text{C}$ ) may explain  
415 their very low abundance that year. Brodeur et al. (2017) reported that the biomass of *C.*  
416 *melanaster* was high around SLI during both warm and cold periods. This suggests that around  
417 SLI, conditions are suitable for the growth of *C. melanaster* polyps. Regarding annual differences  
418 in the oceanographic conditions of this region between 2017 and 2018, the sea ice retreated in April  
419 during 2018, which was approximately 1 month earlier than in 2017 (see Appendix F which is  
420 derived from Arctic Data archive System (ADS) (<https://ads.nipr.ac.jp/>). As previously noted,  
421 early ice retreat may induce late phytoplankton blooms, the dominance of small-sized copepods, and  
422 low productivity, severely affecting food availability for *C. melanaster* (Brodeur et al., 2008). As

423 the sea ice began to retreat faster in 2018 compared with 2017, food conditions were likely to have  
424 been poor for the survival and growth of the ephyrae of *C. melanaster*. The ephyrae of *C.*  
425 *melanaster* grow in the spring to become medusae in summer and reach their peak level of biomass  
426 in autumn (Zavolokin et al., 2008). Thus, the lower numbers of *C. melanaster* in 2018 may be  
427 related to poor food conditions for their ephyra larvae, which in turn, may be related to the early ice  
428 retreat that year.

429 The ctenophores, *B. infundibulum* and *Beroe* sp., which dominated in this region, spend  
430 their entire life cycle in the plankton. Thus, annual differences in food conditions are experienced  
431 during their early juvenile life-history phases. The main food for small ctenophores and ephyrae of  
432 scyphomedusae is copepods (Purcell, 1991). Thus, the timing of the ice retreat underlies annual  
433 differences in food conditions: early ice retreat leads to low productivity with a dominance of small  
434 copepods, whilst late ice retreat leads to high productivity due to the dominance of large copepods  
435 (Brodeur et al., 2008). For ctenophores and scyphomedusae in this region, low standing stocks in  
436 2018 may be related to low productivity of large copepods, which was caused by the early ice retreat  
437 in that year.

438

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590 **Table and figure captions**

591 Table 1. Results of generalized additive models (GAM) based on the abundance of ctenophores  
592 and scyphomedusae (*Bolinopsis infundibulum*, *Chrysaora melanaster*, *Beroe* sp.), and  
593 environmental parameters: depth, temperature, salinity, the effect of pycnocline (U: upper),  
594 day/night, and species interactions of other jellyfishes. +: positive, -: negative, \*:  $p < 0.05$ ,  
595 \*\*:  $p < 0.01$ , \*\*\*:  $p < 0.001$ . Detailed patterns between each parameter are presented in  
596 Fig. 11.

597 Fig. 1. Location of the stations used to observe ctenophores and scyphomedusae by frame camera  
598 in the northern Bering Sea in 9–22 July 2017 (left) and 2–12 July 2018 (right). Numbers in  
599 italics denote the depth strata in meters.

600 Fig. 2. Captured images (A): *Bolinopsis infundibulum* (a), *Chrysaora melanaster* (b), *Beroe* sp. (c).  
601 Frame camera (B): video camera (a), current fin (b), weight (20 kg x 4) (c), observation  
602 frame (d), halogen light (x 2) (e), electronic data cable (f). Schema shows the calculation  
603 of the observed volume (C). For details, see the text.

604 Fig. 3. Temperature (upper) and salinity (lower) cross-sections at each line set in the northern Bering  
605 Sea during 9–22 July 2017. The location of each line is shown in the upper-right map.

606 Fig. 4. Temperature (upper) and salinity (lower) cross-sections at each line set in the northern  
607 Bering Sea during 2–12 July 2018. The location of each line is shown in the upper-right  
608 map.

609 Fig. 5. Horizontal distribution of standing stock (ind. m<sup>-2</sup>) of *Bolinopsis infundibulum* (left),  
610 *Chrysaora melanaster* (middle), and *Beroe* sp. (right) in the northern Bering Sea during 9–  
611 22 July 2017 (upper) and 2–12 July 2018 (lower).

612 Fig. 6. Diel changes in the vertical distribution of *Bolinopsis infundibulum* at four stations (St. 10,  
613 14, 20, 23) in the northern Bering Sea during 9–22 July 2017. Thick bars represent the  
614 distribution core ( $D_{25\%}$ – $D_{75\%}$ ) split with the distribution centre ( $D_{50\%}$ ). Thin bars show the  
615 ranges of  $D_{10\%}$  and  $D_{90\%}$ . Horizontal black bars at the top indicate night-time samplings.  
616 Shaded zones represent the sea bottom. Triangles represent pycnocline depths. Details of  
617 each observation are presented in Appendix C (St. 10) and Appendix D (Sts. 14, 20, 23).

618 Fig. 7. Vertical distribution of temperature, salinity, and *Bolinopsis infundibulum* in the northern  
619 Bering Sea during 9–22 July 2017. Triangles represent pycnocline depths.

620 Fig. 8. Vertical distribution of temperature, salinity and *Chrysaora melanaster* in the northern  
621 Bering Sea during 9–22 July 2017. Triangles represent pycnocline depths.

622 Fig. 9. Vertical distribution of temperature, salinity and *Beroe* sp. in the northern Bering Sea  
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624 Fig. 10. T-S diagrams of all stations in 2017 (left) and 2018 (right) (A). Abundance (ind. m<sup>-3</sup>) of  
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626 Fig. 11. Result of the generalized additive model (GAM) based on abundance anomalies of three  
627 large gelatinous zooplankton with environmental parameters.

628 Appendix A (Table). Data for ctenophores and scyphomedusae observations in the northern Bering  
629 Sea during 9–22 July 2017 and 2–12 July 2018. One cast required approximately 20 min.

630 To evaluate day-night differences, 11 observations were made at 1 h intervals at St. 10 from

631 19:40 13 July to 7:10 14 July 2017. During that period, seven day (19:40, 21:15, 23:12,

632 0:15, 6:10, 7:10) and four night (1:12, 2:13, 3:12, 4:13) casts were made. Observed

633 volume (m<sup>3</sup>) and total counts of each species are also shown for each cast.

634 Appendix B (Figure). Scatter plot on the density of *Bolinopsis infundibulum* quantified during  
635 descent and ascent.

636 Appendix C (Figure). Diel changes in the vertical distribution of *Bolinopsis infundibulum* at St. 10  
637 during 13–14 July 2017. Open and solid markers represent day and night, respectively.

638 Appendix D (Figure). Day (open) and night (solid) vertical distribution of *Bolinopsis infundibulum*  
639 at St. 14, 20, 23 during 17–21 July 2017.

640 Appendix E (Figure). Contour plots for abundance anomalies of three large gelatinous zooplankton  
641 on a T-S diagram.

642 Appendix F (Figure). Sea ice concentration on April 1st in 2017 (left) and 2018 (right). Images

643 were downloaded from the Arctic Data archive System (ADS) (<https://ads.nipr.ac.jp/>).

644 Video supplemental material 1: Example of video image captured at St. 10 (cast 14) on 14 July

645 2017.

646 Video supplemental material 2: Example of video image captured at St. 19 (cast 27) on 19 July

647 2017.

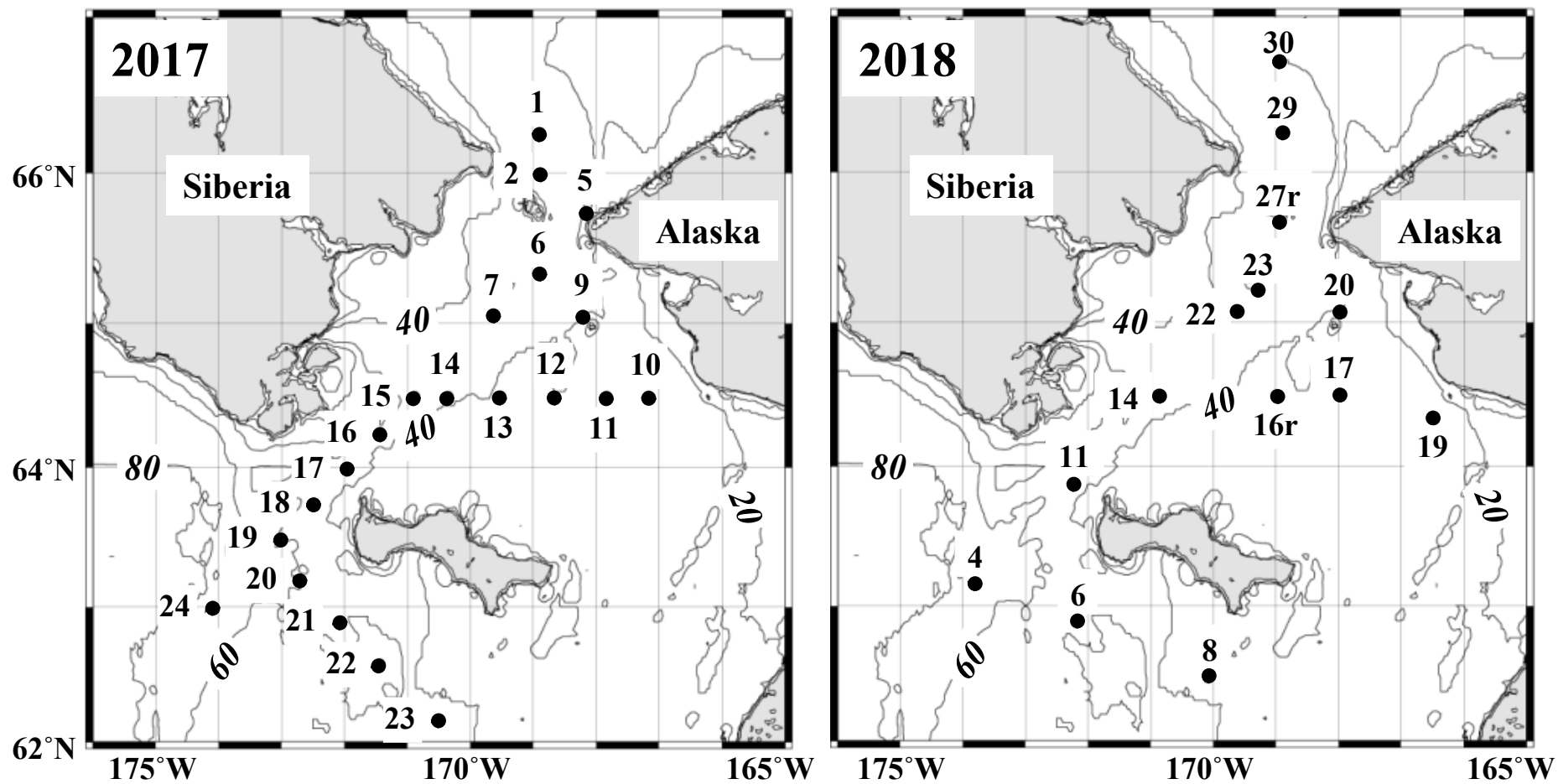
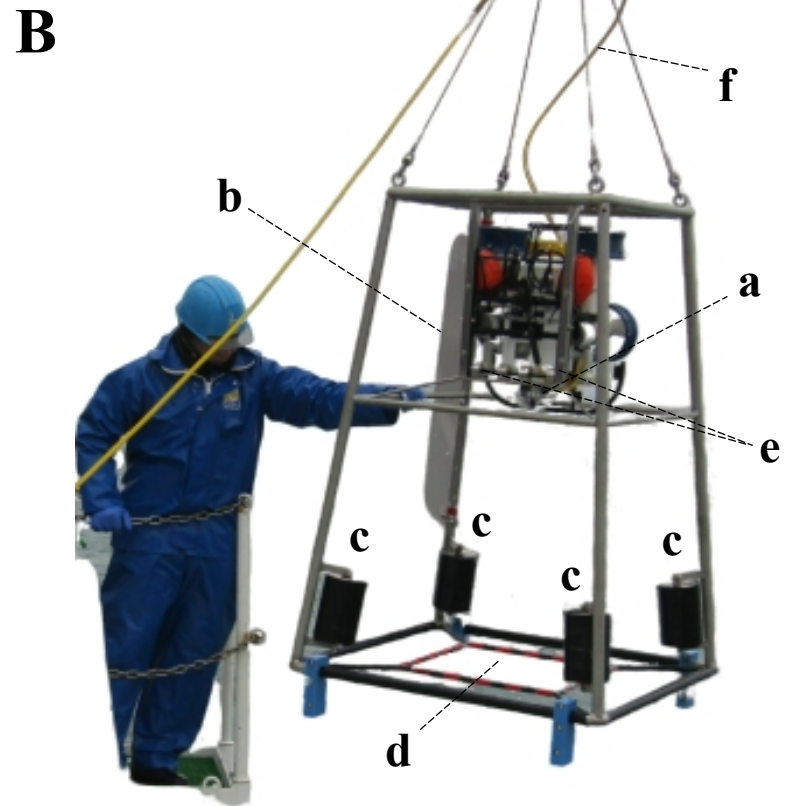
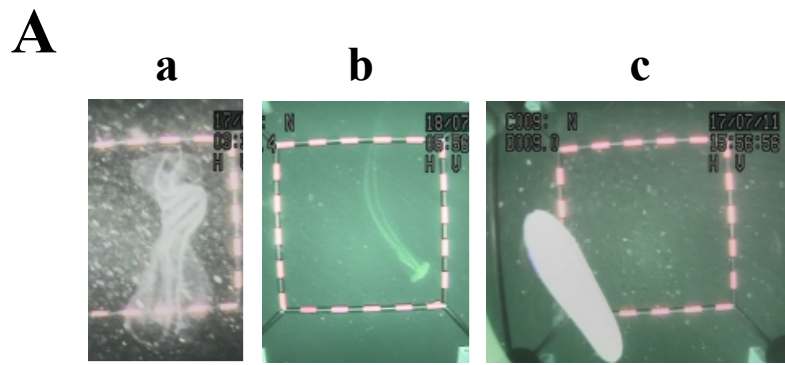


Fig. 1. Location of the stations used to observe ctenophores and scyphomedusae by frame camera in the northern Bering Sea in 9–22 July 2017 (left) and 2–12 July 2018 (right). Numbers in italics denote the depth strata in meters.





**C**

**Observation volume (m<sup>3</sup>)**

$$= 2 \times 1.2 \times 0.8 \times \boxed{20 \times 1/Pt}$$

Observed Field (m<sup>3</sup>)
Time (s)
Horizontal drifting of view at one second

*Pt*: passage time within the observation field (s)

☐: Effect of horizontal advection

**Effect of horizontal advection by current**

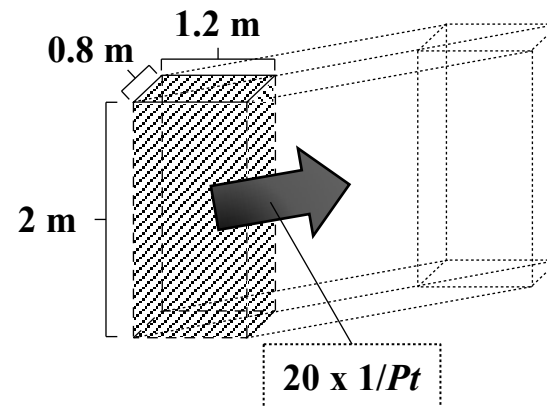


Fig. 2. Captured images (A): *Bolinopsis infundibulum* (a), *Chrysaora melanaster* (b), *Beroe* sp. (c). Frame camera (B): video camera (a), current fin (b), weight (20 kg x 4) (c), observation frame (d), halogen light (x 2) (e), electronic data cable (f). Schema shows the calculation of the observed volume (C). For details, see the text.

2017

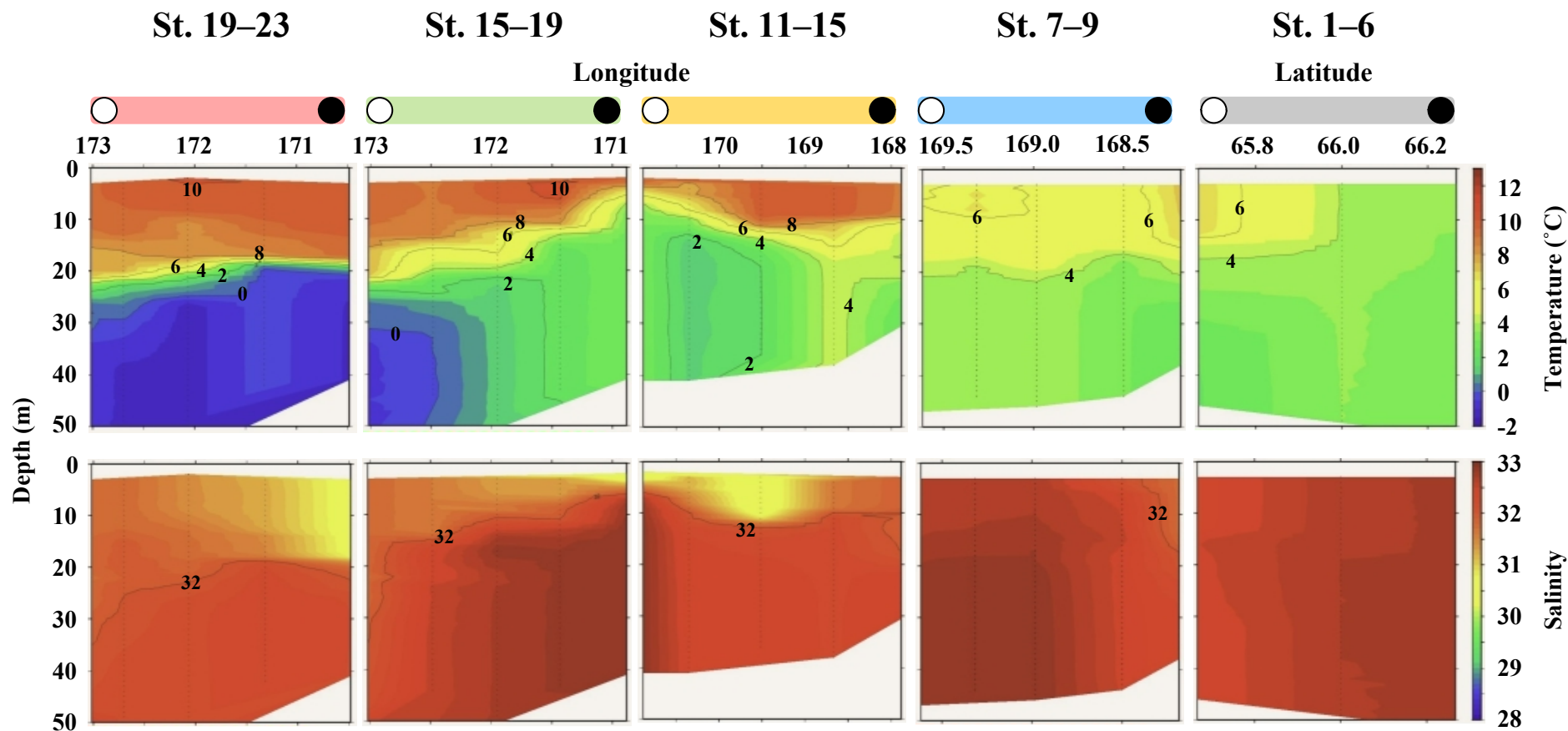
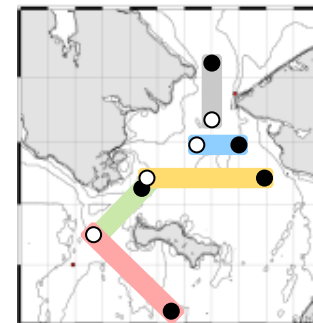


Fig. 3. Temperature (upper) and salinity (lower) cross-sections at each line set in the northern Bering Sea during 9–22 July 2017. The location of each line is shown in the upper-right map.

2018

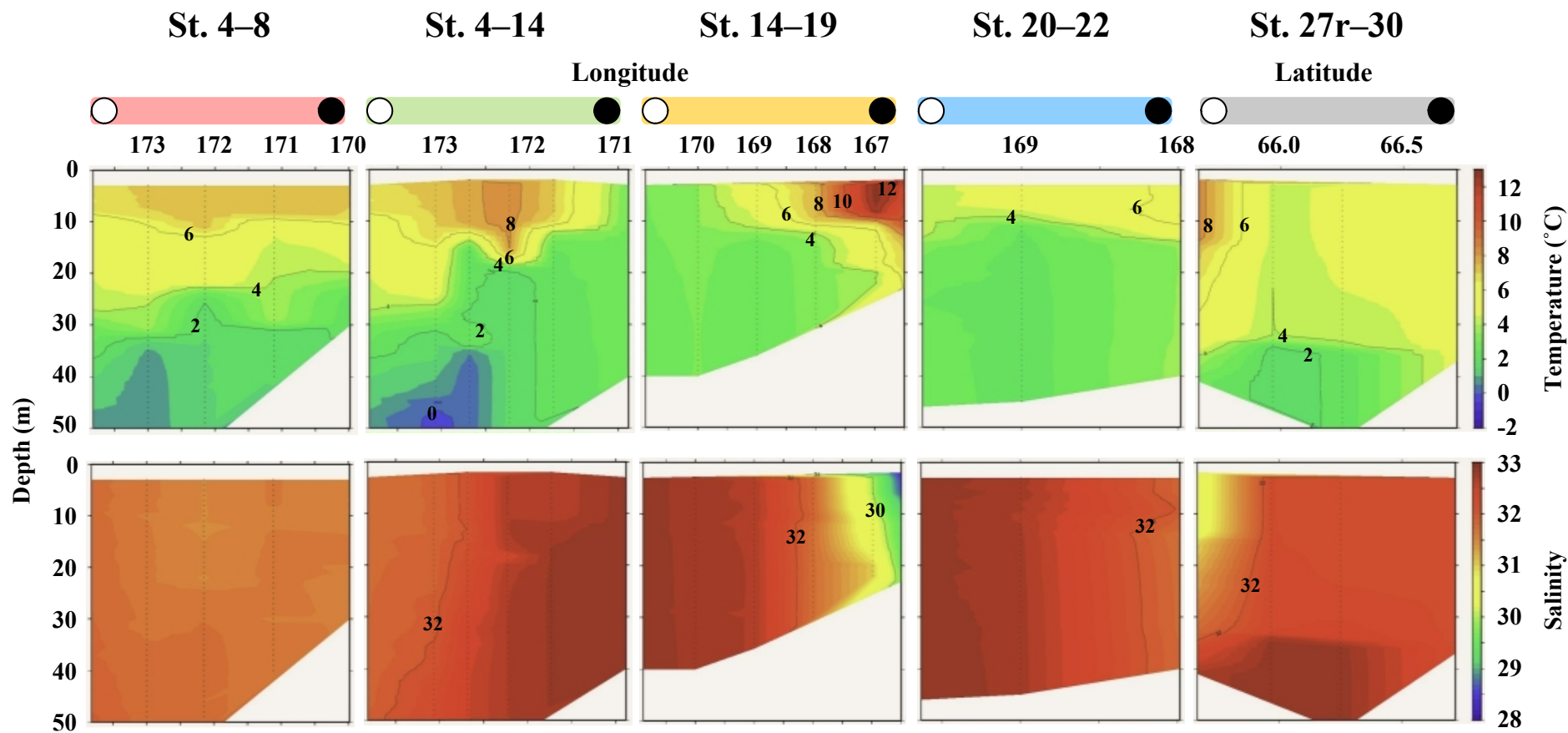
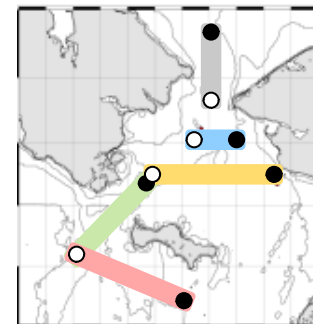


Fig. 4. Temperature (upper) and salinity (lower) cross-sections at each line set in the northern Bering Sea during 2–12 July 2018. The location of each line is shown in the upper-right map.

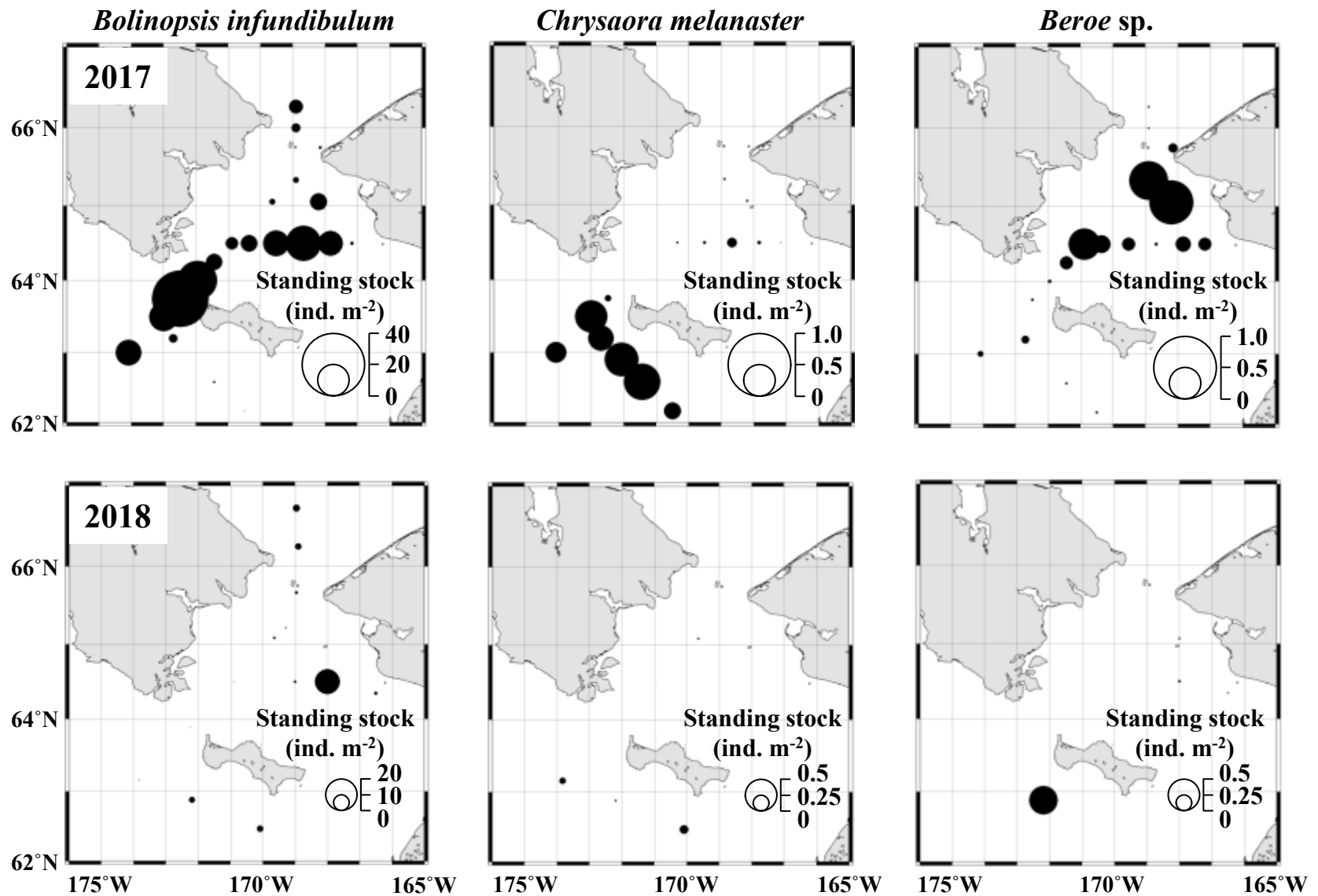


Fig. 5. Horizontal distribution of standing stock (ind. m<sup>-2</sup>) of *Bolinopsis infundibulum* (left), *Chrysaora melanaster* (middle), and *Beroe sp.* (right) in the northern Bering Sea during 9–22 July 2017 (upper) and 2–12 July 2018 (lower).

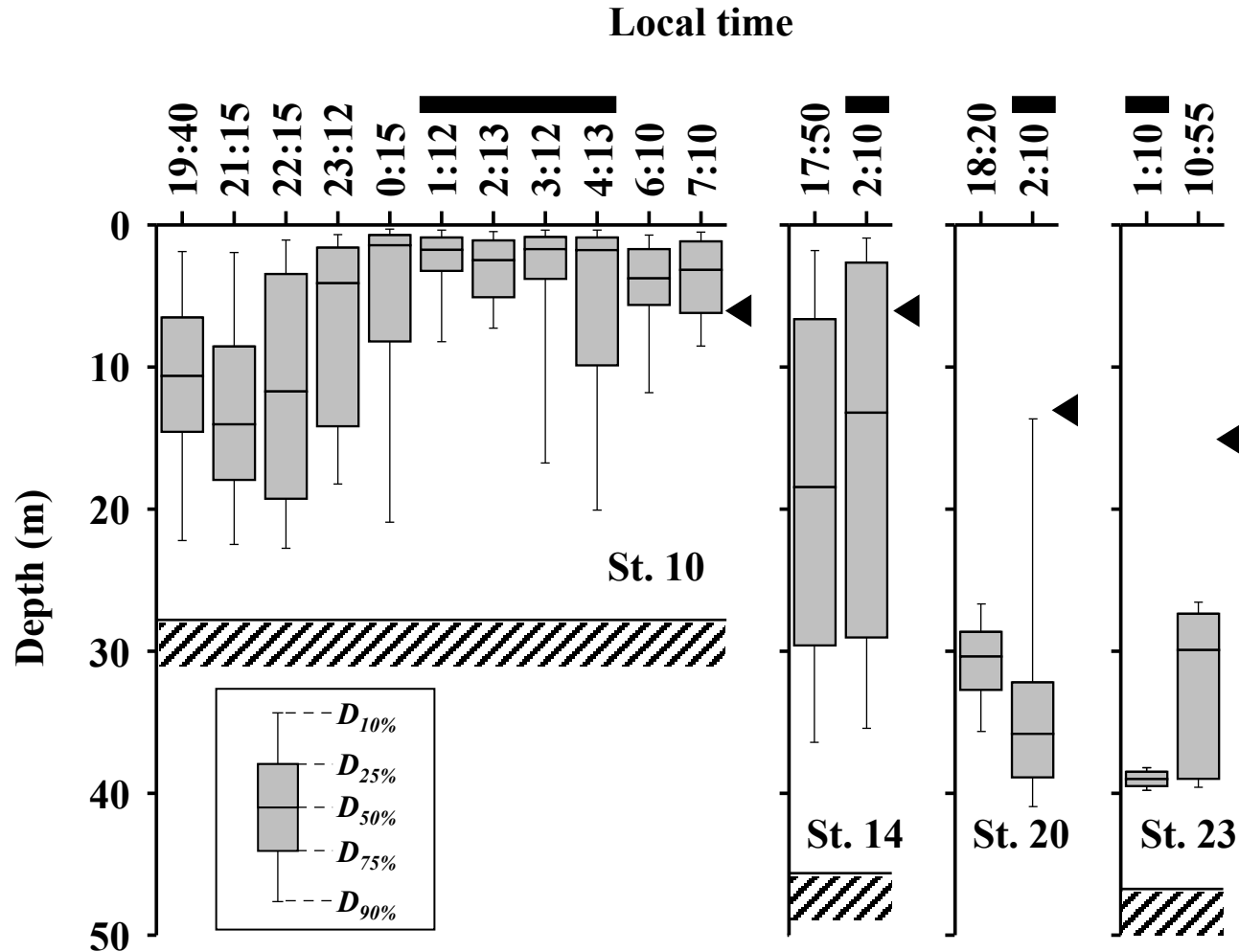


Fig. 6. Diel changes in the vertical distribution of *Bolinopsis infundibulum* at four stations (St. 10, 14, 20, 23) in the northern Bering Sea during 9–22 July 2017. Thick bars represent the distribution core ( $D_{25\%} - D_{75\%}$ ) split with the distribution centre ( $D_{50\%}$ ). Thin bars show the ranges of  $D_{10\%}$  and  $D_{90\%}$ . Horizontal black bars at the top indicate nighttime samplings. Triangles represent pycnocline depths. Details of each observation are presented in Electronic Supplement 1 (St. 10) and 2 (Sts. 14, 20, 23).

2017

*Bolinopsis infundibulum*

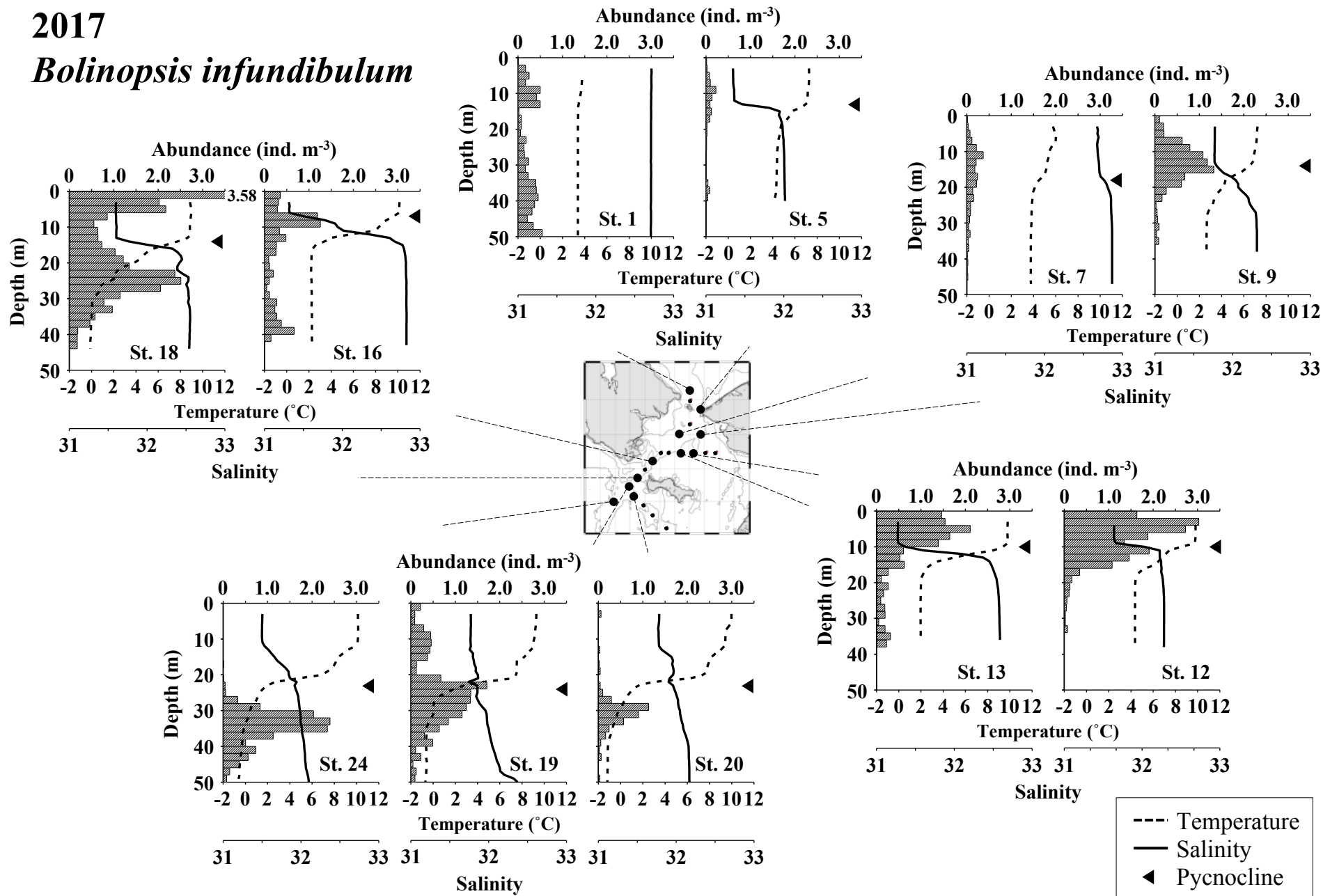


Fig. 7. Vertical distribution of temperature, salinity, and *Bolinopsis infundibulum* in the northern Bering Sea during 9–22 July 2017. Triangles represent pycnocline depths.

# 2017 *Chrysaora melanaster*

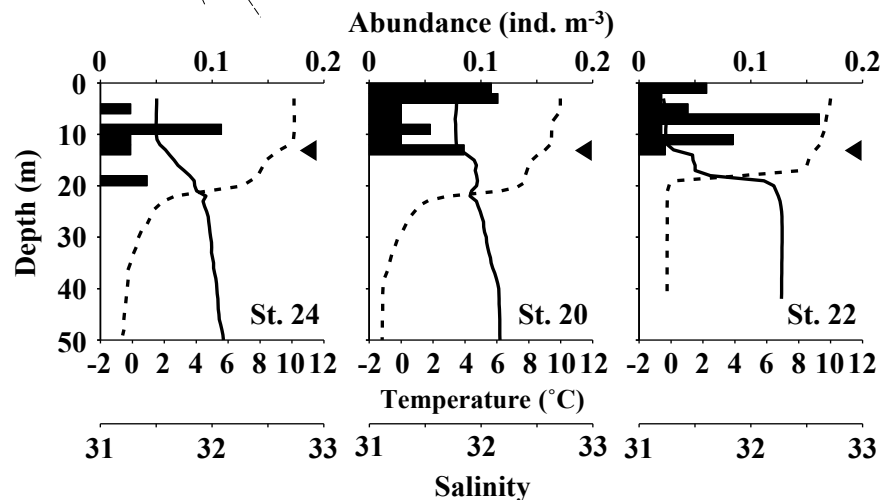
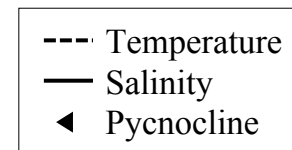
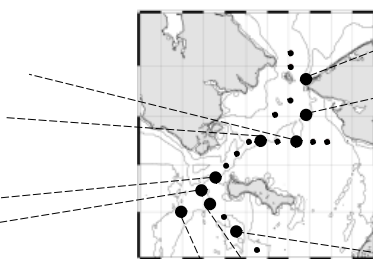
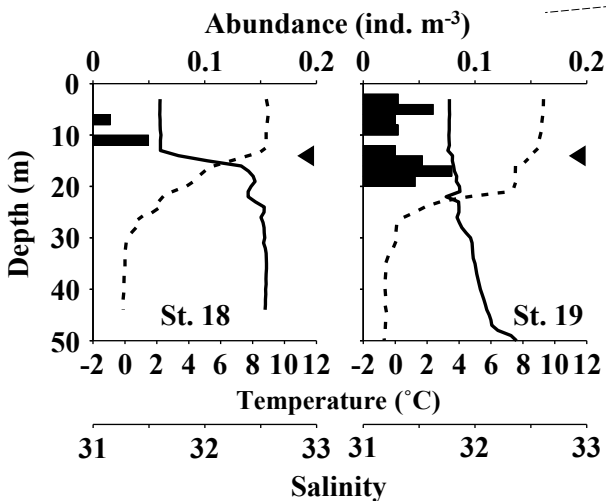
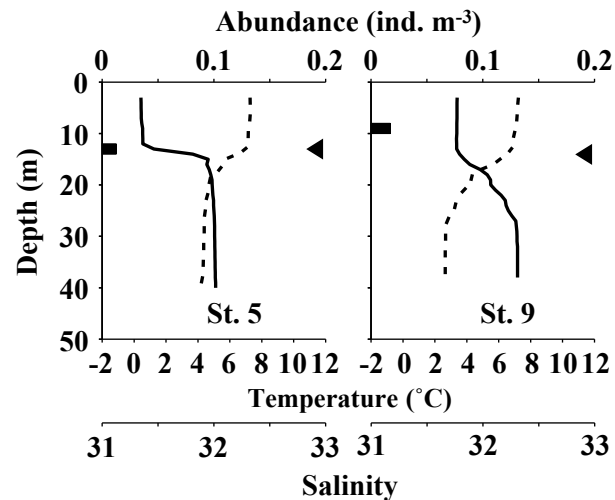
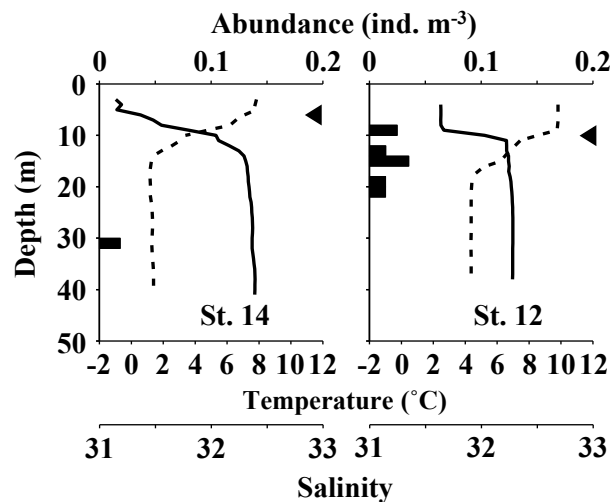


Fig. 8. Vertical distribution of temperature, salinity and *Chrysaora melanaster* in the northern Bering Sea during 9–22 July 2017. Triangles represent pycnocline depths.

# 2017 *Beroe* sp.

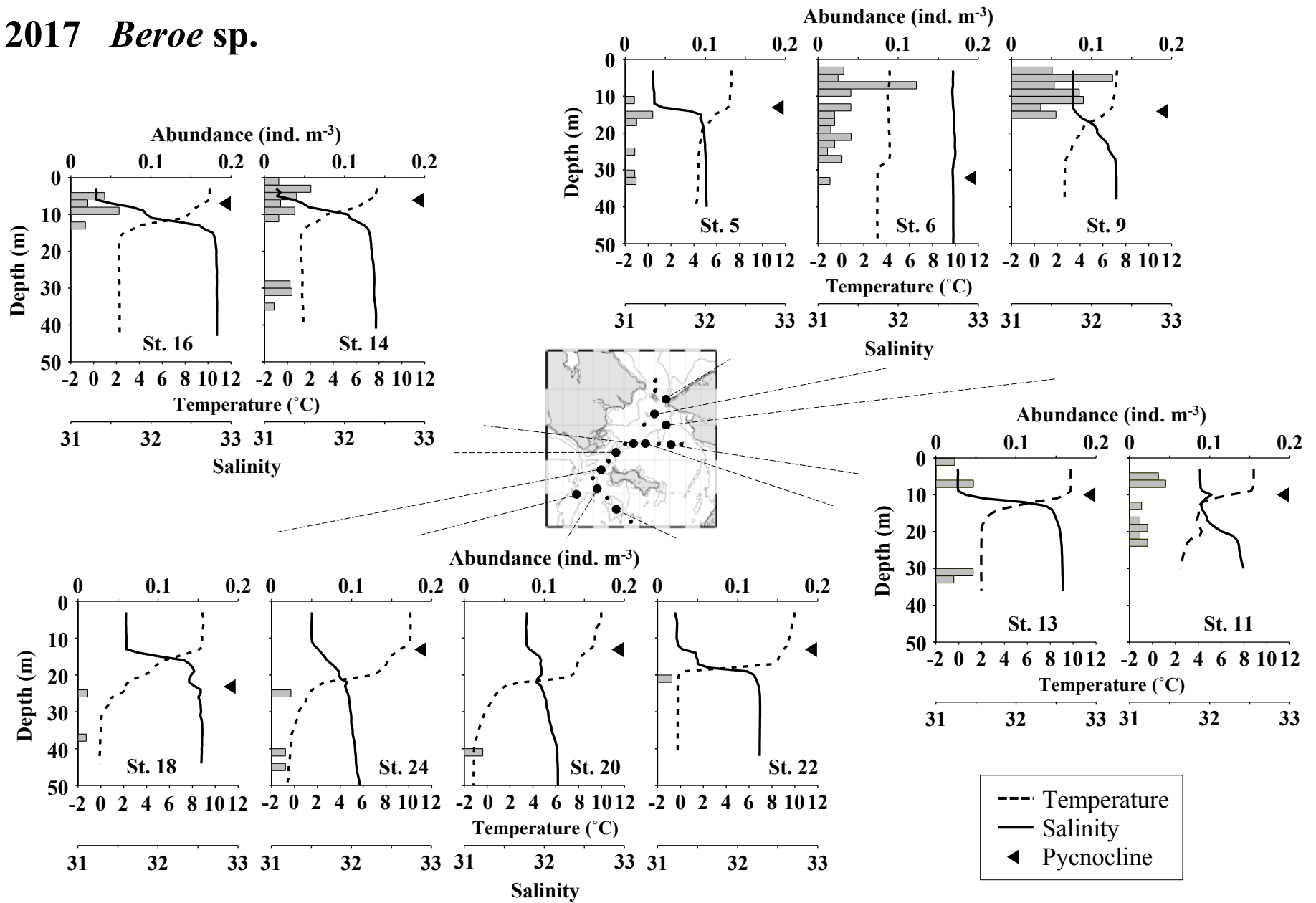


Fig. 9. Vertical distribution of temperature, salinity and *Beroe* sp. in the northern Bering Sea during 9–22 July 2017. Triangles represent pycnocline depths.



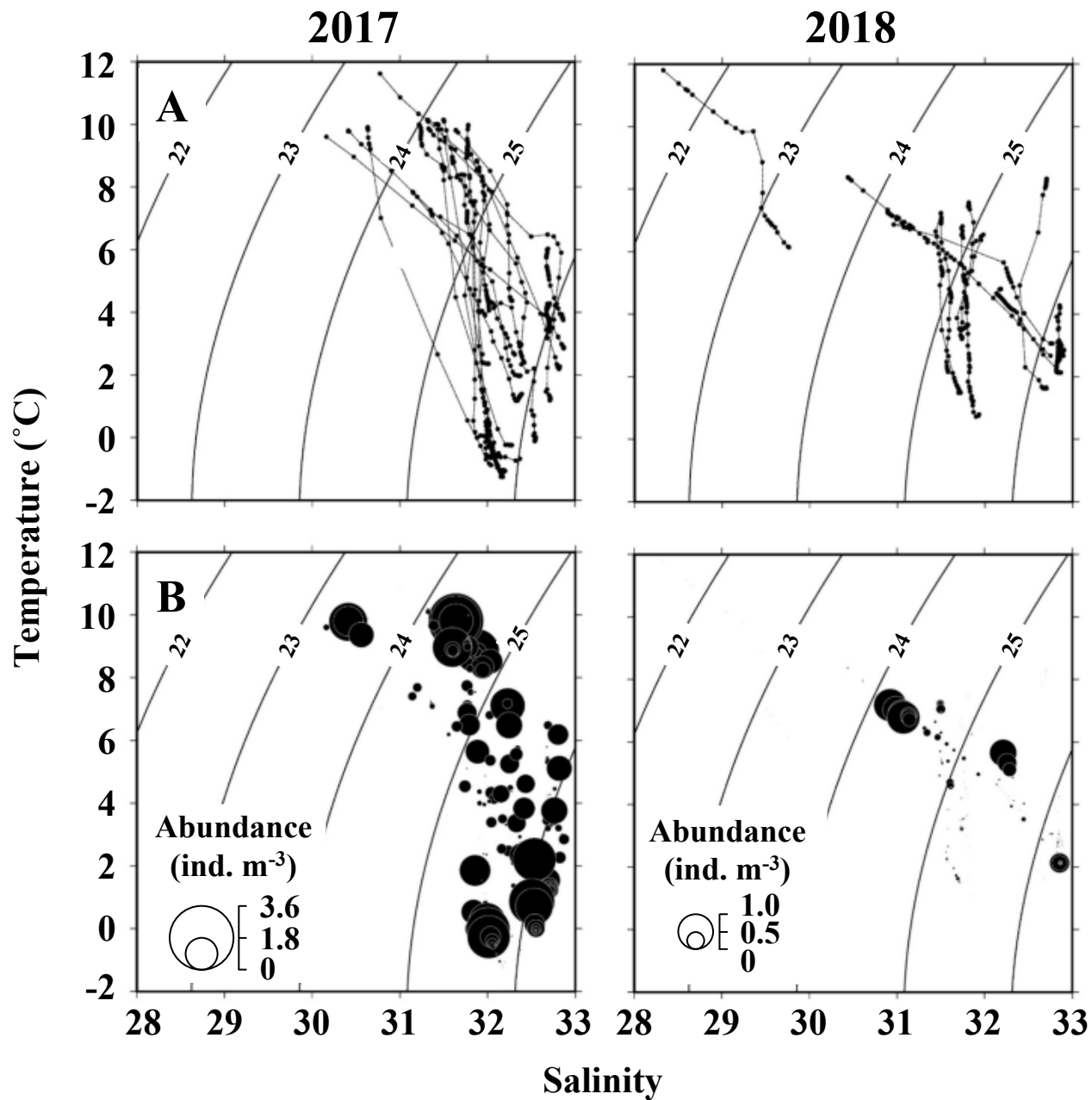


Fig. 10. T-S diagrams of all stations in 2017 (left) and 2018 (right) (A). Abundance (ind. m<sup>-3</sup>) of *Bolinopsis infundibulum* at 2 m intervals is shown by bubble plots on T-S diagrams (B).

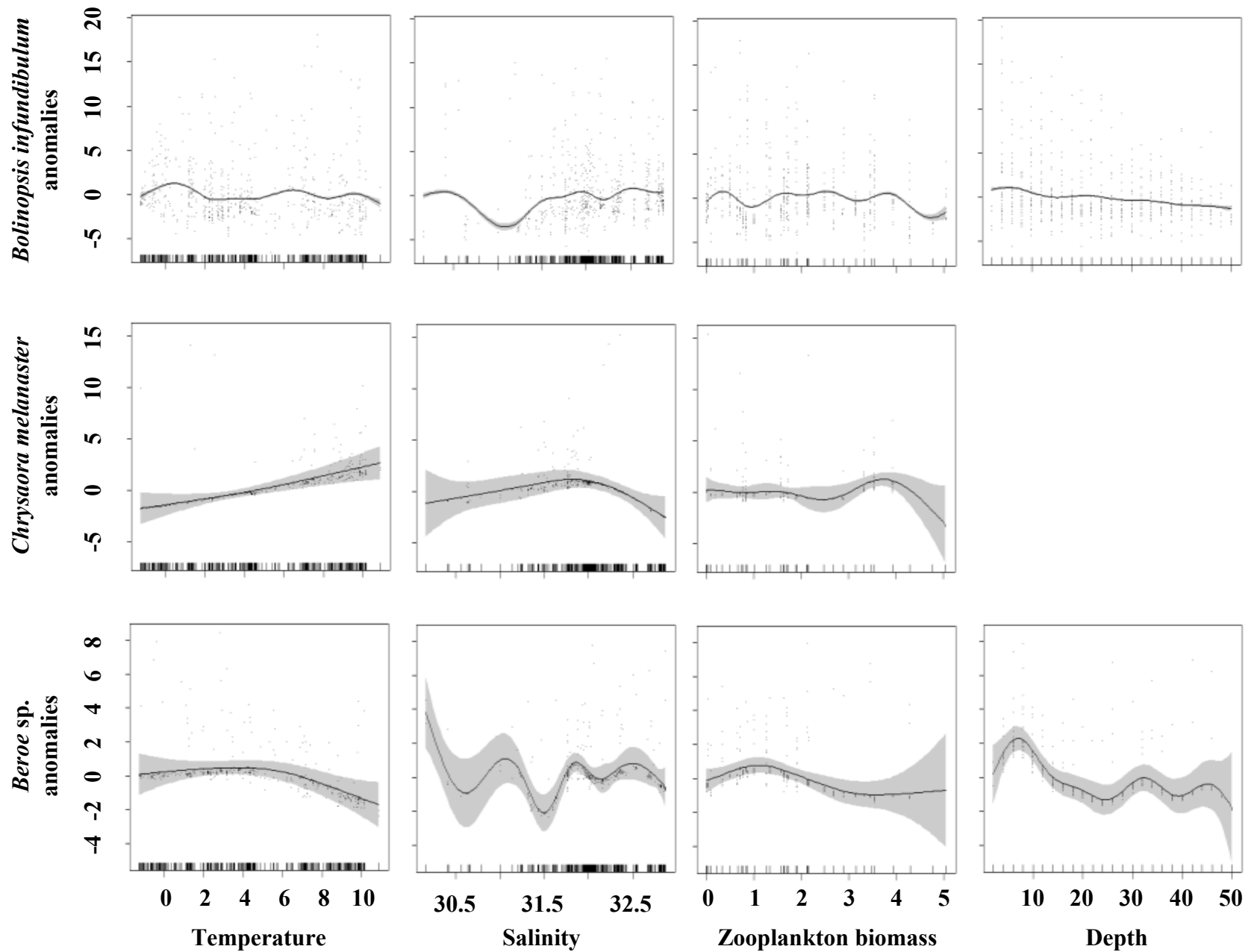
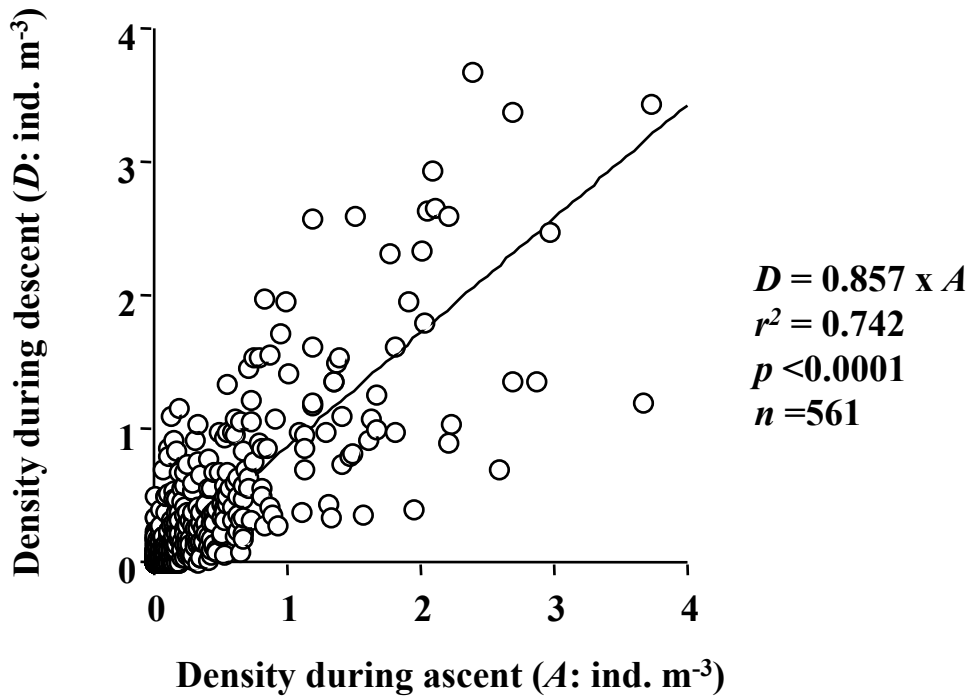


Fig. 11. Result of generalized additive model (GAM) based on abundance anomalies of three large gelatinous zooplankton with environmental parameters.

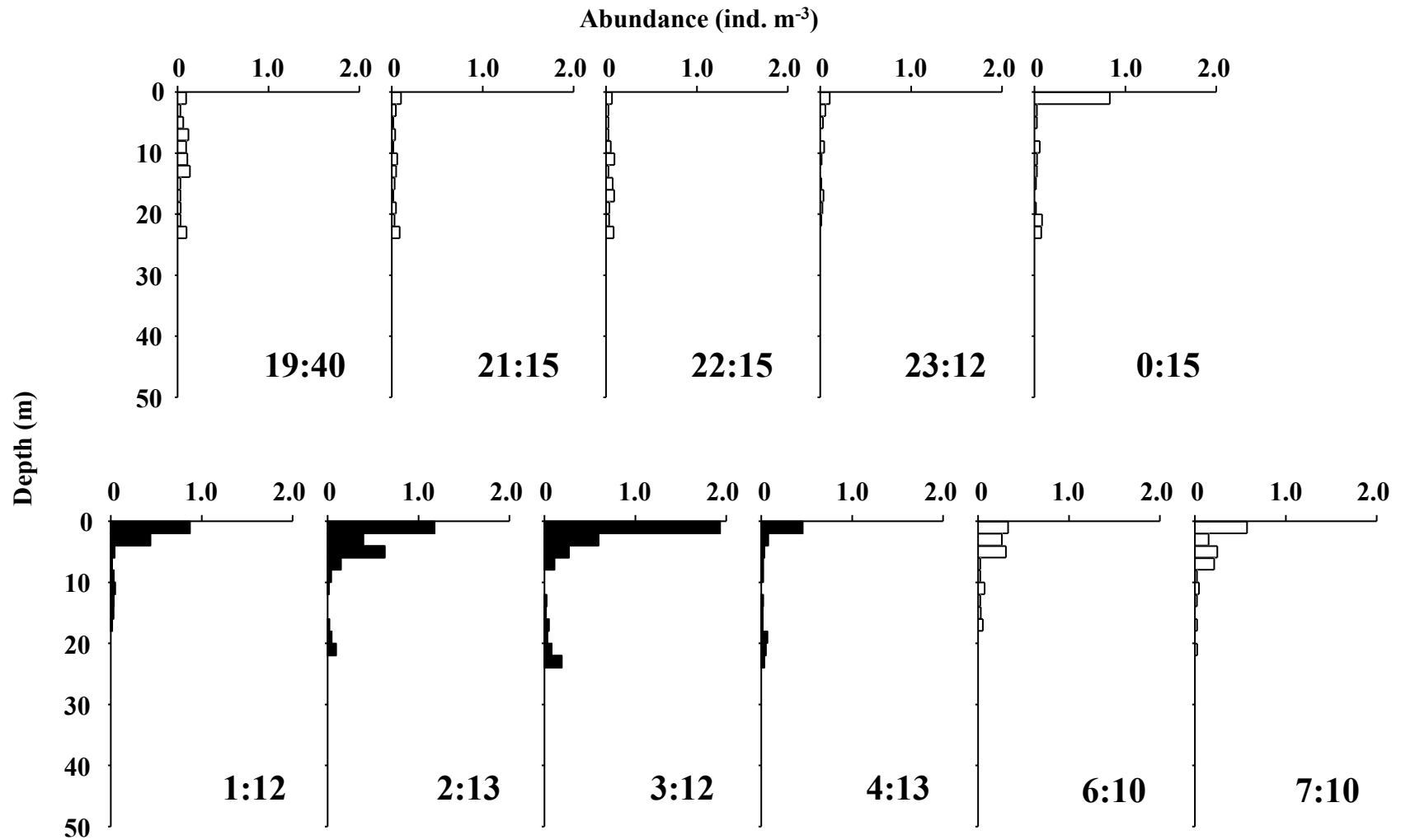
Appendix A. Data for ctenophores and scyphomedusae observations in the northern Bering Sea during 9–22 July 2017 and 2–12 July 2018. One cast required approximately 20 min. To evaluate day-night differences, 11 observations were made at 1 h intervals at St. 10 from 19:40 13 July to 7:10 14 July 2017. During that period, seven day (19:40, 21:15, 23:12, 0:15, 6:10, 7:10) and four night (1:12, 2:13, 3:12, 4:13) casts were made. Observed volume (m<sup>3</sup>) and total counts of each species during descent and ascent of each cast are also shown.

Year	Station (depth m)	Cast	Position		Local time		Day/night	Descent				Ascent			
			Lat. (N)	Lon. (W)	Date	Hour		Observed volume (m <sup>3</sup> )	<i>B. infundibulum</i>	<i>C. melanaster</i>	<i>Beroe</i> sp.	Observed volume (m <sup>3</sup> )	<i>B. infundibulum</i>	<i>C. melanaster</i>	<i>Beroe</i> sp.
2017															
	1 (57)	1	66°16'	168°54'	9 July	13:00	Day	677.8	221	0	1	688.9	111	0	0
	2 (53)	2	66°00'	168°54'	10 July	3:40	Night	1105.4	215	0	0	1069.1	177	0	1
	5 (44)	3	65°45'	168°09'	11 July	9:00	Day	701.9	59	1	2	818.1	17	0	5
	6 (55)	4	65°20'	168°54'	11 July	16:30	Day	780.5	77	0	10	946.0	113	1	13
	7 (51)	5	65°03'	169°38'	12 July	8:45	Day	995.0	89	0	0	934.6	100	0	0
	9 (42)	6	65°03'	168°12'	13 July	10:00	Day	697.8	262	1	20	620.8	163	0	8
	10 (28)	7	64°30'	167°10'	13 July	19:40	Day	496.0	48	0	2	492.6	15	0	3
	10 (28)	8	64°30'	167°10'	13 July	21:15	Day	547.2	35	0	9	475.4	15	0	7
	10 (28)	9	64°30'	167°10'	13 July	22:15	Day	428.4	16	0	1	340.7	14	0	5
	10 (28)	10	64°30'	167°10'	13 July	23:12	Day	478.2	20	0	9	274.3	3	0	3
	10 (28)	11	64°30'	167°10'	14 July	0:15	Day	508.4	25	0	5	438.0	58	0	2
	10 (28)	12	64°30'	167°10'	14 July	1:12	Night	459.5	30	0	0	297.4	35	0	5
	10 (28)	13	64°30'	167°10'	14 July	2:13	Night	452.6	62	0	5	272.0	73	0	2
	10 (28)	14	64°30'	167°10'	14 July	3:12	Night	342.6	93	0	7	297.1	44	1	7
	10 (28)	15	64°30'	167°10'	14 July	4:13	Night	430.4	18	0	3	357.0	27	0	6
	10 (28)	16	64°30'	167°10'	14 July	6:10	Day	282.9	32	0	5	250.6	15	0	4
	10 (28)	17	64°30'	167°10'	14 July	7:10	Day	285.3	43	0	3	305.9	18	0	2
	11 (34)	18	64°30'	167°50'	16 July	20:12	Day	615.9	400	1	6	504.9	300	1	4
	12 (42)	19	64°30'	168°40'	17 July	3:50	Night	710.2	549	3	2	475.3	320	2	0
	13 (40)	20	64°30'	169°31'	17 July	11:40	Day	425.4	161	0	5	361.3	271	1	1
	14 (46)	21	64°30'	170°21'	17 July	17:50	Day	609.2	227	1	5	651.0	279	0	10
	14 (46)	22	64°30'	170°21'	18 July	2:10	Night	724.2	146	0	4	815.5	304	1	5
	15 (45)	23	64°30'	170°53'	18 July	10:50	Day	677.3	187	0	17	521.8	116	0	4
	16 (47)	24	64°15'	171°26'	18 July	16:40	Day	680.5	206	0	2	569.9	197	0	5
	17 (53)	25	64°00'	171°57'	18 July	21:50	Day	935.0	783	0	0	889.6	487	0	2
	18 (48)	26	63°45'	172°29'	19 July	3:50	Night	870.1	1026	1	2	880.8	861	3	0
	19 (65)	27	63°30'	173°00'	19 July	10:55	Day	661.7	324	6	0	522.8	283	7	0
	20 (66)	28	63°12'	172°42'	19 July	18:20	Day	658.7	79	7	0	561.1	109	9	1
	20 (66)	29	63°12'	172°42'	20 July	2:10	Night	731.5	69	3	4	678.7	130	3	4
	21 (54)	30	62°54'	172°04'	20 July	10:35	Day	548.4	0	7	0	480.3	0	7	0
	22 (47)	31	62°35'	171°26'	20 July	18:45	Day	520.7	12	17	1	427.5	18	3	0
	23 (46)	32	62°10'	170°30'	21 July	1:10	Night	518.2	1	1	0	404.7	0	5	0
	23 (46)	33	62°10'	170°30'	21 July	10:55	Day	330.2	2	3	1	510.5	1	6	0
	24 (76)	34	63°00'	174°05'	22 July	1:30	Night	645.3	295	6	1	527.1	251	2	2
2018															
	4 (76)	35	63°09'	173°50'	2 July	14:08	Day	1144.5	3	2	0	928.4	3	3	0
	6 (56)	36	62°53'	172°12'	3 July	1:34	Night	875.9	44	0	5	928.1	94	0	13
	8 (36)	37	62°28'	170°05'	3 July	12:50	Day	515.9	56	3	0	334.1	31	0	0
	11 (55)	38	63°53'	172°15'	4 July	14:58	Day	794.8	1	0	0	750.9	2	0	0
	14 (46)	39	64°30'	170°54'	5 July	1:20	Night	704.3	1	0	0	646.8	0	0	0
	17 (35)	40	64°30'	168°00'	5 July	14:54	Day	279.9	10	0	0	487.6	33	0	0
	19 (28)	41	64°21'	166°30'	5 July	21:56	Day	294.7	0	0	0	247.6	0	0	0
	20 (45)	42	65°04'	168°00'	6 July	6:48	Day	512.0	11	0	0	656.3	15	0	0
	22 (52)	43	65°05'	169°39'	6 July	16:40	Day	588.7	6	0	0	392.4	2	0	0
	23 (49)	44	65°13'	169°18'	7 July	21:58	Day	711.0	39	0	0	706.5	91	0	0
	30 (42)	45	66°44'	168°58'	11 July	0:50	Day	652.9	14	0	0	475.6	17	0	0
	29 (56)	46	66°15'	168°54'	11 July	10:18	Day	575.4	10	0	0	571.8	22	0	0
	27r (46)	47	65°40'	168°58'	11 July	21:37	Day	397.1	59	0	0	619.5	51	0	0
	16r (41)	48	64°30'	169°00'	12 July	9:30	Day	305.4	164	0	0	244.7	36	0	0

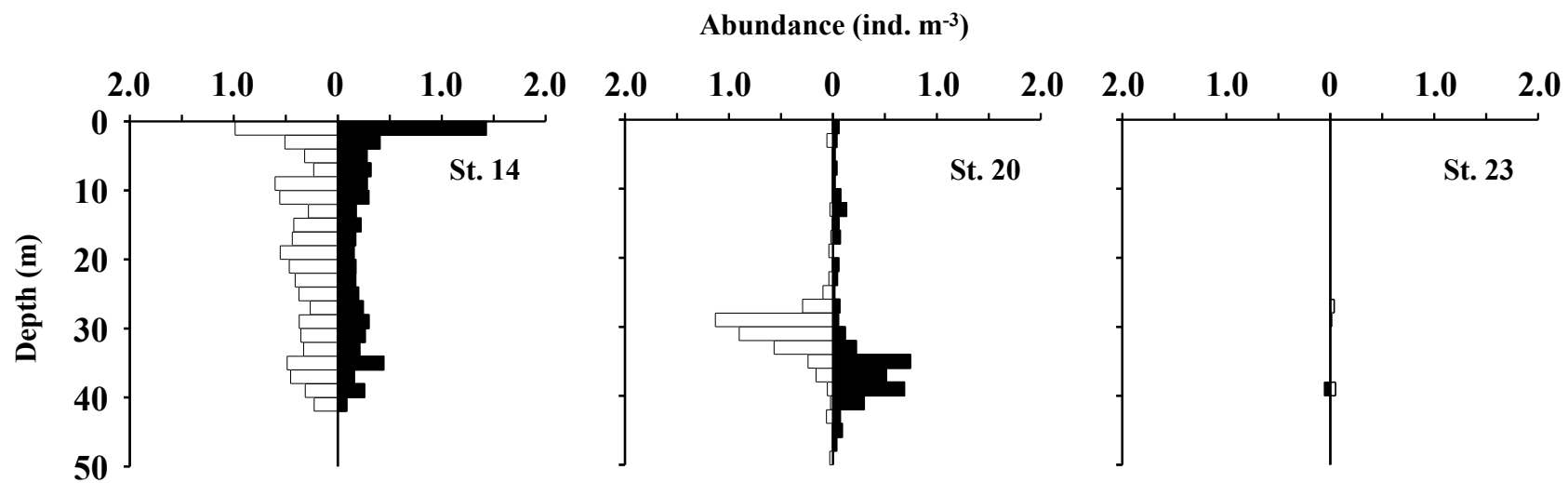
**Abundance of *Bolinopsis infundibulum***



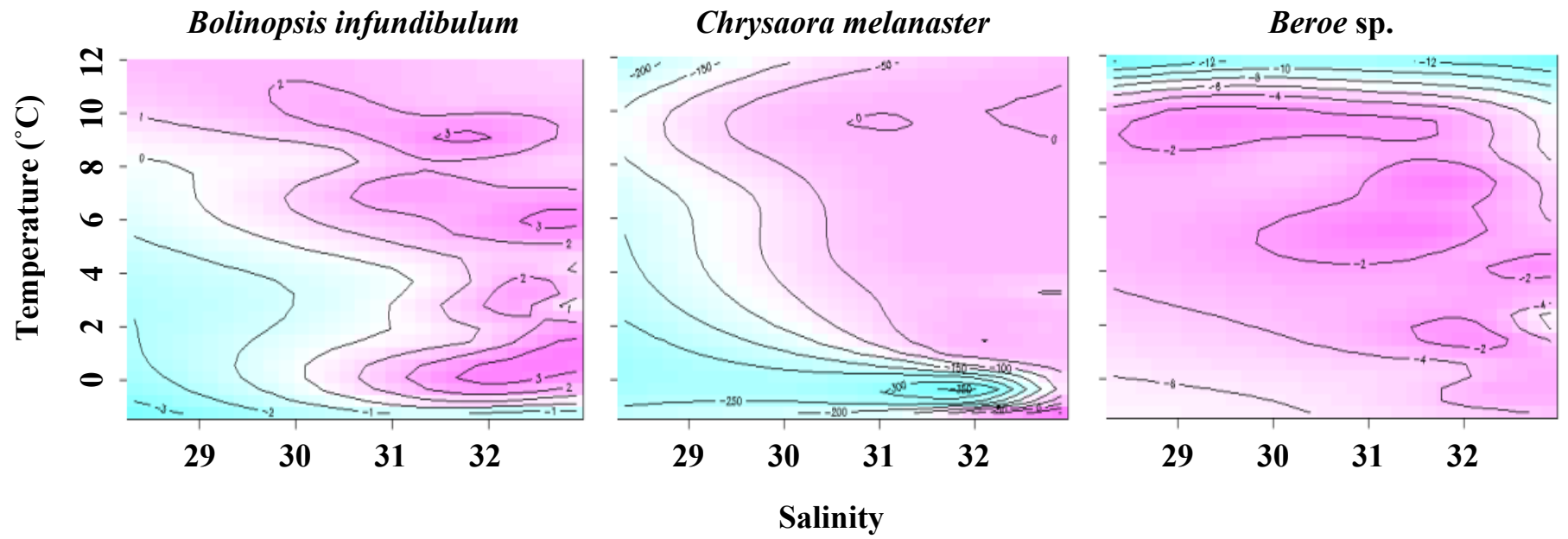
Appendix B. Scatter plot on the density of *Bolinopsis infundibulum* quantified during descent and ascent.



Appendix C. Diel changes in the vertical distribution of *Bolinopsis infundibulum* at St. 10 during 13–14 July 2017. Open and solid markers represent day and night, respectively.



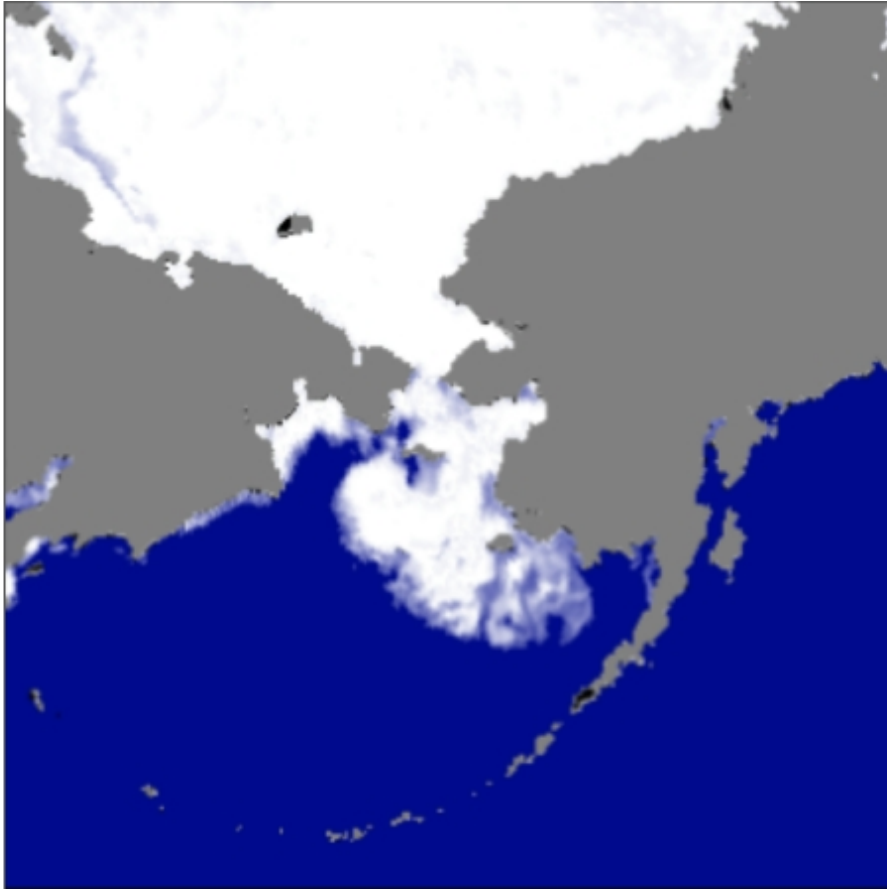
Appendix D. Day (open) and night (solid) vertical distribution of *Bolinopsis infundibulum* at St. 14, 20, 23 during 17–21 July 2017.



Appendix E. Contour plots for abundance anomalies of three large gelatinous zooplankton on a T-S diagram.

## Sea ice concentration

2017/04/01



2018/04/01



Appendix F. Sea ice concentration on April 1st in 2017 (left) and 2018 (right). Images were downloaded from Arctic Data archive System (ADS) (<https://ads.nipr.ac.jp/>).