

Between-year comparison of interactions between environmental parameters and various plankton stocks in the northern Bering Sea during the summers of 2017 and 2018

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ABSTRACT

In the northern Bering Sea, ice coverage and retreat timing were low and early, respectively, in the 2017–2018 winter. To evaluate the effect of these anomalous ice conditions, we quantified various environmental parameters (temperature, salinity, mixed-layer depth, nutrients) and the standing stocks of various planktonic taxa (phytoplankton counts, meso- and macrozooplankton mass, jellyfish abundance) during July of 2017 and 2018. For each year, the interaction between each parameter was evaluated by structural equation modelling (SEM) analysis. Large yearly differences were detected for the interactions between environmental parameters and planktonic stocks. Thus, for 2017, a total of fifteen interactions were present between environmental parameters and various planktonic stocks. In 2018, however, only eight interactions were present. Among the interactions, four were common to the two years. It is notable that the path coefficients of these four interactions were all lower in 2018 than in 2017. These findings suggest that the small magnitude and short pulse of the phytoplankton bloom in 2018 may have failed to transfer production and energy to a higher trophic level even within the planktonic food web. Indeed, in 2018, mass mortality was reported for seabirds (two murre species) feeding on planktivorous fishes.

1. Introduction

In the northern Bering Sea, the sea ice coverage area for the 2017–2018 winter was reported to be at the minimum level recorded by satellite observations initiated in 1978 (Cornwall, 2019). For seabirds, mass mortality of two murre species (common murre and thick-billed murre) and reproductive failure of two auklet species (crested auklet and least auklet) were reported during the summer of 2018 (Dragoo et al., 2019; Duffy-Anderson et al., 2019). Lack of food resources and warming sea temperature are possible causes of mass seabird mortality and reproductive failure (Jones et al., 2018, 2019). In a normal year, more than 70% of the area of the southern shelf region of the St. Lawrence Island is covered by a cold pool characterized by < 2 °C bottom temperature (cf. Stabeno and Bell, 2019). However, the cold pool was absent in the summer of 2018, and the extent of the northern

distribution limit of pelagic fish fauna was affected (Cornwall, 2019; Duffy-Anderson et al., 2019). For recent years, changes in horizontal distribution of walrus and frequency and seasonal duration of whales are also reported (Jay et al., 2017; Stafford, 2019). Consequently, through changes in timing shifts in marine mammal hunting and whaling, there is a large effect on the life of indigenous people (Huntington et al., 2020). Despite the pronounced between-year difference in the sea-ice conditions, temperature, fishes, sea-bird and marine mammals in 2017–2019 (Huntington et al., 2020), little information is available concerning the mechanisms and interactions between environmental variables and the planktonic food web.

The evaluation of the mechanisms and effects of low ice coverage and early ice retreat on the marine ecosystem in the northern Bering Sea is similar to an effort to gather pieces of a puzzle that vary between taxa, regions, and years and attempting to provide a highly likely hypothesis

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that explains the whole phenomenon. For the evaluation of these mechanisms, there are three principal approaches. The first is the horizontal characterization of pelagic biota, which varied with the target area (Questel et al., 2013; Ershova et al., 2015a). The second is to perform comparisons between years with great differences in environmental and ice conditions (Matsuno et al., 2011; Pinchuk and Eisner, 2017). Third, the comparison of recent biotic conditions with historical conditions applying historical data archives has been successful for zooplankton and seabirds (Ershova et al., 2015b; Gall et al., 2017). This method is direct, and accurate evaluation of yearly differences may be possible by considering yearly differences in methodology (station, mesh size, quantification method, unit of stock [abundance or biomass]), but this method is inevitably limited to certain targeted taxa. Bearing in mind the above three approaches, the structural equation modeling (SEM) analysis is a powerful tool to evaluate interactions between environmental parameters and plankton stocks (Matsuno et al., 2016; Amano et al., 2019).

In the present study, we evaluate the mechanisms by which yearly differences in ice conditions may affect various plankton stocks using SEM analysis based on directly obtained environmental (temperature, salinity, mixed-layer depth, nutrients, fluorescence) and plankton stock

(phytoplankton, meso- and macro-zooplankton biomass, jellyfish abundance) data during July of 2017 and 2018.

2. Materials and methods

During the 40th and 56th cruises of the T/S *Oshoro-Maru* (Hokkaido University), environmental measurements and plankton stock assessment were performed at 21 stations (2017) and 13 stations (2018) in the northern Bering Sea from 9–22 July 2017 and 2–12 July 2018 (Fig. 1). All the stations were located at 62°10'N–66°44'N latitude and 174°05'W–166°30'W longitude, and their water depths were 27–76 m. For each station, temperature, salinity, and fluorescence were measured by CTD (Sea-bird Electronics 911Plus) and fluorescence sensor (Seapoint Sensors, Inc.). Mixed layer depth (MLD) was defined as the depth where the seawater density was increased by 0.1 kg m⁻³ from that at 5 m depth (Danielson et al., 2011). Water samples from 10-m intervals throughout the water column were frozen, and nutrients (NO₃⁻, NO₂⁻, NH₄⁺, PO₄³⁻, Si(OH)₄) were measured with an autoanalyser QuAatro 2-HR system (BL-tec, Osaka, Japan; Seal Analytical, Norderstedt, Germany). These environmental parameters were calculated with depth-averaged or depth-integrated values at each station. Thus, we abbreviated as

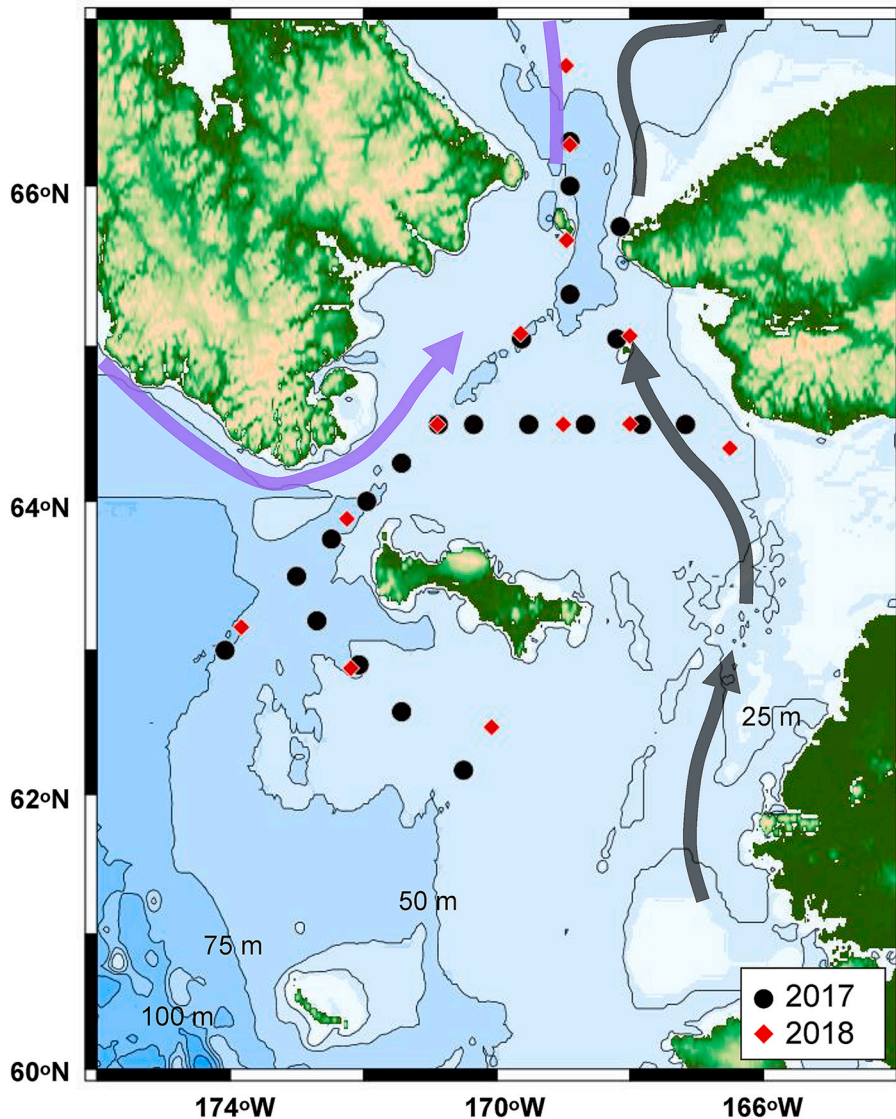


Fig. 1. Location of the sampling stations in 2017 and 2018 along with the bathymetry and main circulation patterns (Danielson et al., 2017). Purple: Anadyr Current; Black: Alaskan Coastal Current.

following: depth-averaged temperature (T: °C), depth-averaged salinity (S), depth-integrated fluorescence (Flu), depth-integrated nitrate + nitrite (NO_x: μM), ammonium (NH₄: μM), phosphate (P: μM), silicate (Si: μM).

For phytoplankton, 500–1000 mL water samples collected at each depth were preserved with 1% glutaraldehyde and concentrated to 24- to 50-fold, and diatoms and dinoflagellates were examined for 1-mL subsamples mounted on glass slides with an inverted microscope with 40–600x magnification. Phytoplankton stock was integrated throughout the water column and expressed as $\times 10^6$ cells m⁻² (abbreviated as Phyto). For mesozooplankton, samples were collected from vertical hauls of a flowmeter-mounted NORPAC net (45-cm mouth diameter equipped with 335-μm mesh). For macrozooplankton, samples were collected by oblique hauls of a flowmeter-mounted Bongo net (70-cm diameter with 505-μm mesh). These zooplankton samples were preserved in borax-buffered 5% formalin-seawater, and their wet masses were measured with a precision of 0.1 mg using a microbalance (Mettler-Toledo). Masses of mesozooplankton (Meso) and macrozooplankton (Macro) were expressed as standing stock of the water column (g WM m⁻²). The abundance of macro-to mega-sized jellyfish was quantified at 1-m depth intervals from video images captured by slow vertical tows (0.1 m s⁻¹) of the video camera (Marine Arkas, Kowa Co. Ltd) down to the 50-m depth at each station. For the quantification of jellyfish, the

effect of horizontal advection was also considered (Marie Maekakuchi, personal communication). Jellyfish abundance in 1-m intervals was integrated over the 0–50 m water column, then expressed as the standing stock (Jelly: ind. m⁻²).

To evaluate interactions between each environmental parameter and plankton stock, SEM analysis was performed for each year (Grace, 2006; Grace et al., 2010). Through SEM analysis, interactions between parameters composing ecosystems are evaluated as positive or negative path coefficients (Grace et al., 2010). For SEM analysis, environmental parameters (T, S, and MLD) were set at the first row. Nutrients (NO_x, NH₄, P, and Si) and plankton (Flu, Phyto, Meso, and Macro) were set at the second and third rows, respectively. Jelly was set for the fourth row. Subsequently, the parameters characterized by non-significant relations ($p > 0.05$) with the other parameters (P, Si, Flu and Macro) were removed from the final model. The overall fit of the final model was evaluated by the goodness-of-fit index (GFI) and the adjunct goodness-of-fit index (AGFI). The SEM analysis was performed using add-in software for MS-Excel (<http://www.ohmsha.co.jp/data/link/978-4-274-06925-3/>).

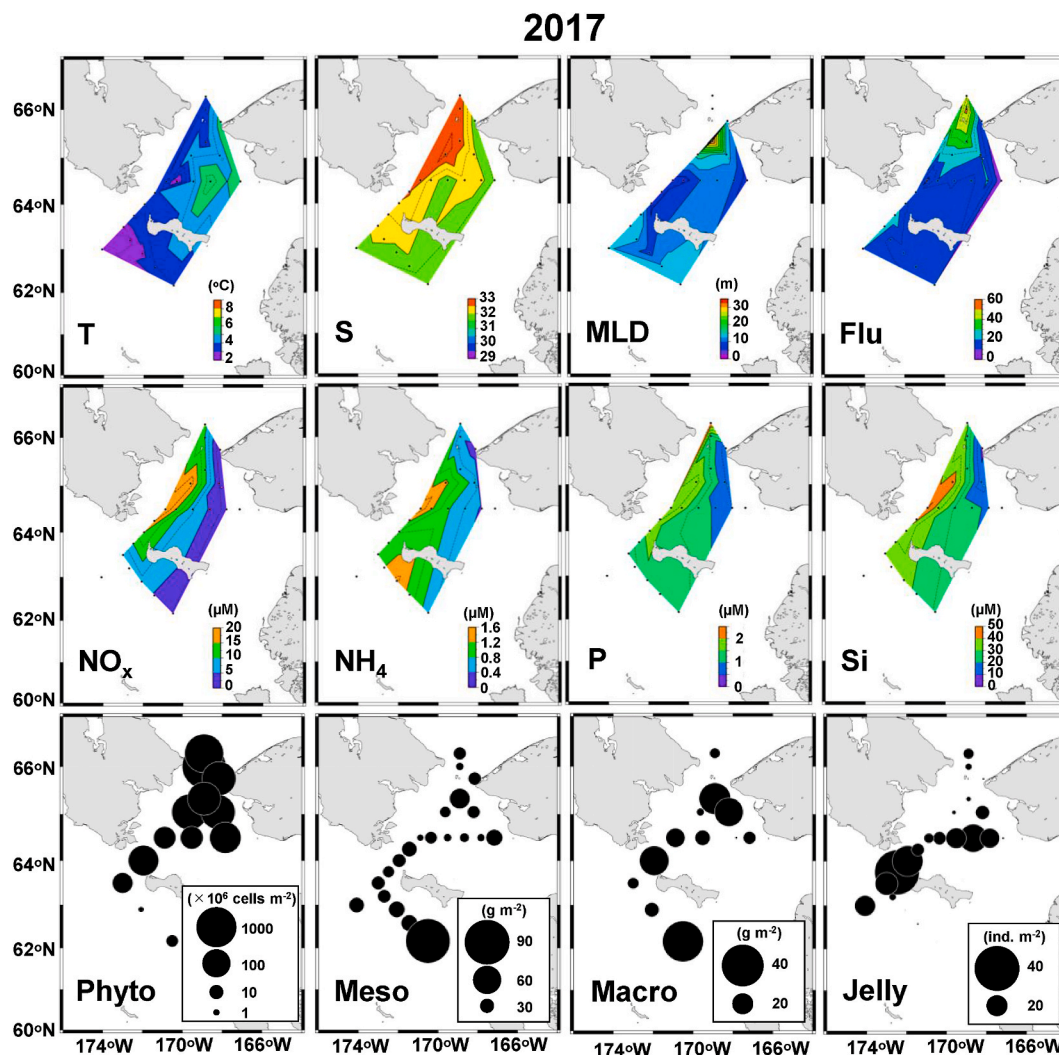


Fig. 2. Horizontal distribution of depth-averaged temperature (T), salinity (S), mixed-layer depth (MLD), depth-integrated fluorescence (Flu), nitrate + nitrite (NO_x), ammonia (NH₄), PO₄ (P), SiO₄ (Si), phytoplankton cell stock (Phyto), wet mass of mesozooplankton (Meso), wet mass of macrozooplankton (Macro), and jellyfish standing stock (Jelly) in the northern Bering Sea during July of 2017.

3. Results

3.1. Horizontal distribution

The horizontal distributions of various environmental parameters and various plankton stocks in 2017 and 2018 are shown in Figs. 2 and 3, respectively. In both years, T and S had opposite gradients for the east-west direction. Thus, T ranged from 2.1 to 8.5 °C and was high at the eastern side (Alaska). On the other hand, S ranged from 29.4 to 32.9 and was high for the western side (Siberia). MLD and Flu exhibited north-south gradients (Figs. 2 and 3). MLD was at 6–33 m and was deeper at the northern side (Chukchi Sea). Flu ranged from 4.9 to 52.4 (arbitrary units) and was higher for the northern side (Chukchi Sea). Nutrients (NO_x, NH₄, PO₄, SiO₄) showed pronounced east-west gradients; thus they were higher for the western side (Siberia) and lower for the eastern side (Alaska). These east-west patterns were prominent in 2017, while NH₄ in 2018 showed a relatively high value even at the Alaskan side (Fig. 3). Phyto was high near the Bering Strait in 2017. Meso ranged from 5.29 to 88.93 g WM m⁻², Macro (expressed in the same units) ranged from 0.27 to 40.82 g WM m⁻², and Meso was significantly higher than Macro throughout the region and in both years (*p* < 0.01, *U* test). A high between-year difference was detected for Jelly; thus Jelly was significantly higher in 2017 (mean 10.54 ± 2.03 ind. m⁻²) than in 2018

(2.53 ± 1.15 ind. m⁻²) (*p* < 0.01, *U* test).

3.2. SEM analysis

The results of SEM analysis between environmental parameters and various classes of plankton stock in 2017 and 2018 are shown in Fig. 4. The most prominent difference between the two years was that the number of interactions was greater in 2017 than in 2018. Thus, fifteen interactions were present between environmental parameters and various plankton stocks in 2017, while only eight interactions were detected in 2018 (Fig. 4). Among the interactions, four were common in both years (Table 1, colored red in Fig. 4). Thus, negative interactions were present between temperature and NH₄, NH₄ and Phyto, and Phyto and Jelly, while positive interaction was observed for salinity and NO_x. The path coefficients of these four common interactions were all lower in 2018 than in 2017. Three interactions showed opposite patterns between years. Thus, temperature and Jelly were negatively related in 2017 but positively related in 2018. Salinity and Phyto were positively related in 2017 but negatively related in 2018. For Meso and Jelly, negative (2017) and positive (2018) interactions were detected.

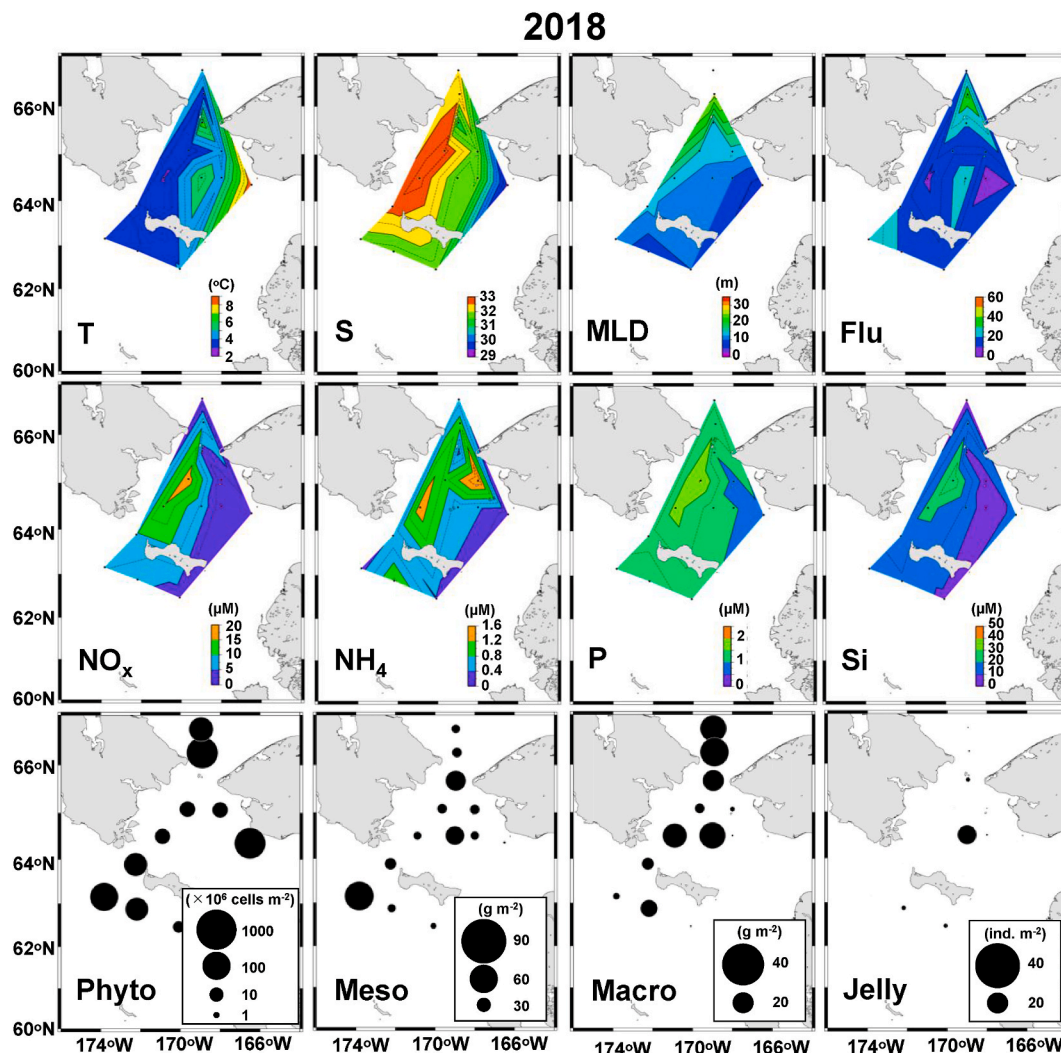


Fig. 3. Horizontal distribution of depth-averaged temperature (T), salinity (S), mixed-layer depth (MLD), depth-integrated fluorescence (Flu), nitrate + nitrite (NO_x), ammonia (NH₄), PO₄ (P), SiO₄ (Si), phytoplankton cell stock (Phyto), wet mass of mesozooplankton (Meso), wet mass of macrozooplankton (Macro), and jellyfish standing stock (Jelly) in the northern Bering Sea during July of 2018.

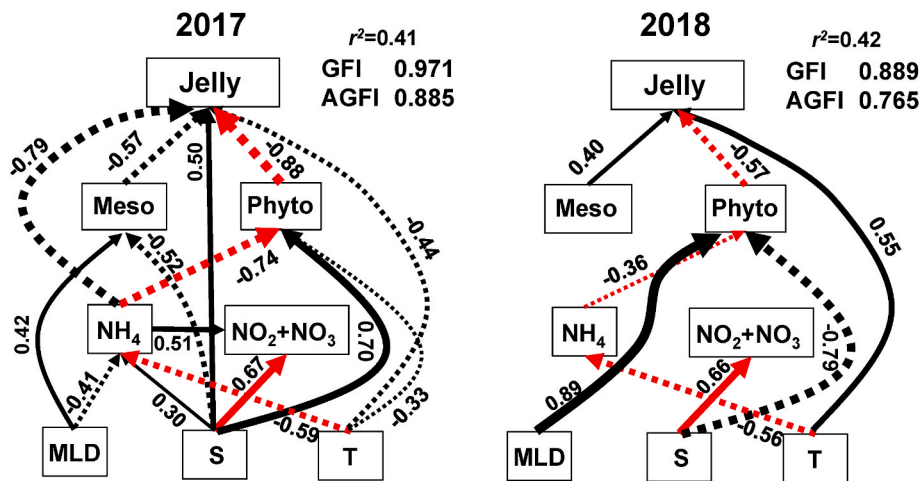


Fig. 4. Results of structural equation model (SEM) analysis between environmental parameters and various plankton taxa in the northern Bering Sea during July of 2017 (left) and 2018 (right). The values along the pathways represent standardized path coefficients. Solid and dashed lines indicate positive and negative relationships, respectively. The four common interactions in both years are colored with red. MLD: mixed-layer depth, S: depth-averaged salinity, T: depth-averaged temperature, Meso: wet mass of mesozooplankton, Phyto: phytoplankton cell standing stock, Jelly: jellyfish standing stock.

Table 1

Significant path coefficients detected between environmental parameters and various plankton stocks in the northern Bering Sea during the summers of 2017 and 2018 (cf. Fig. 4). T: depth-averaged temperature, S: depth-averaged salinity, MLD: mixed-layer depth, NO_x: NO₂+NO₃, Phyto: phytoplankton cell stock, Meso: mesozooplankton biomass, Jelly: jellyfish stock.

Interactions	2017	2018
Common pattern for both year		
T-NH ₄	-0.59	-0.56
S-NO _x	0.67	0.66
NH ₄ -Phyto	-0.74	-0.36
Phyto-Jelly	-0.88	-0.57
Only in 2017		
T-Phyto	-0.33	
S-NH ₄	0.30	
S-MeSo	-0.52	
S-Jelly	0.50	
MLD-NH ₄	-0.41	
MLD-Meso	0.42	
NH ₄ -NO _x	0.51	
NH ₄ -Jelly	-0.79	
Only in 2018		
MLD-Phyto		0.89
Oppose pattern with year		
T-jelly	-0.44	0.55
S-Phyto	0.70	-0.79
Meso-Jelly	-0.57	0.40

4. Discussion

4.1. Horizontal distribution

The horizontal distribution of environmental parameters, phyto- and zoo plankton stocks, and fish communities in this region was extensively studied by the Arctic Ecosystem Integrated Survey (Arctic Eis) (Mueter et al., 2017). The water mass present on the eastern side (Alaska), the Alaskan Coastal Current is characterized as warm and fresh, while the water mass on the western side (Siberia), the Anadyr Current is characterized as cold and saline (Danielson et al., 2017). In the present study, the east-west gradient in T and S may be related to this east-west difference in water masses (Figs. 2 and 3). Horizontal distributions of nutrients and phytoplankton stock in this region are known to have a well parallel with that of water masses (Danielson et al., 2017). Within the water masses in this region, strong current and front between two water masses in Bering Strait lead to strong mixing and deep MLD are reported for the Bering Strait Water (Eisner et al., 2013). In the Bering Strait, the MLD of Bering Strait Water and nutrient-rich Bering Sea Water is known to be weak and deep with high chlorophyll *a* (Danielson et al., 2017).

Horizontal distribution of MLD and Flu found in this study corresponded well with these north-south patterns (Figs. 2 and 3). Diatoms such as *Chaetoceros* spp. were dominated in the phytoplankton community of this region (Fukai et al., 2019).

The most important zooplankton species in mesozooplankton biomass of this region is the copepod *Calanus glacialis* (Ershova et al., 2015a). From the viewpoint of food for higher trophic levels, large-sized Pacific copepods (e.g., *Neocalanus* spp. and *Eucalanus bungii*) are also important (Eisner et al., 2013; Pinchuk and Eisner, 2017). The Pacific copepods are known to be abundant in the Anadyr Current (Pinchuk and Eisner, 2017; Sigler et al., 2017). Within the macrozooplankton, euphausiid *Thysanoessa raschii* is known to be the most important in this region (Eisner et al., 2013). All sampling in this study was conducted during July, which corresponded to the season of the midnight sun. Since euphausiids may perform great diel vertical migration (cf. Mauchline, 1980), they are expected to be distributed in the near-bottom layer during that season. This may explain the lower biomass of Macro than that of Meso (Figs. 2 and 3). As a large dominant jellyfish of this region, scyphomedusa *Chrysaora melanaster* is known to be important (De Robertis and Taylor, 2014). For Jelly, yearly changes were more prominent than horizontal changes. Add to *C. melanaster*, ctenophore *Bolinopsis infundibulum* was the dominant component of jellyfish in this study (Marie Maekakuchi, personal communication).

4.2. Yearly changes in the planktonic food web (SEM analysis)

From SEM analysis, significant interactions between environmental parameters and various plankton stocks were present for fifteen in 2017 but only eight in 2018 (Fig. 4). It is also notable that the path coefficients of the four common interactions of both years were all lower in 2018 than in 2017 (Table 1). These findings suggest that the interactions within the lower trophic level were weak in 2018.

In the study region (northern Bering Sea), the ice coverage area for the 2017–2018 winter was reported to be at a minimum level by satellite observation initiated in 1978 (Cornwall, 2019). This anomalous ice condition was caused by strong southern wind during autumn of 2017, warm winter atmosphere and water, vertical mixing yielding low ice coverage area, and then rapid ice melting in the spring of 2018 (Stabeno and Bell, 2019). Due to these ice conditions, phytoplankton had no ice-edge bloom and weak stratification, and only a small-magnitude open-water spring bloom was reported in 2018 (Duffy-Anderson et al., 2019). For mesozooplankton, dominance of small copepods and a few abundant large copepods, which are important foods for seabirds and higher trophic levels, were reported in 2018 (Duffy-Anderson et al., 2019). Since the cold pool, characterized by low temperature (<2 °C) and normally present for the southern St. Lawrence Island during

summer, was completely absent during summer of 2018, pelagic fishes were reported to extend their distribution into the northern area due to the absence of a northern barrier of the cold pool in 2018 (Cornwall, 2019; Duffy-Anderson et al., 2019). The most prominent changes at higher trophic levels in 2018 were observed for seabirds, where breeding failure occurred for two auklet species (crested auklet and least auklet), and a die-off was reported for two murre species (common murre and thick-billed murre) (Dragoo et al., 2019; Duffy-Anderson et al., 2019). These observations may be related to a small-magnitude open-water spring bloom in 2018. Thus, low primary production and energy would reduce energy and material transfer to higher trophic levels, and the effect might be prominent for the highest trophic level (seabird) in the marine ecosystem. In the present study, the paucity of interactions between environmental variables and plankton stocks in 2018 relative to those in 2017 (Fig. 4) may reflect the lower production of materials and energy in 2018. Since the mesozooplankton wet masses of 2017 were comparable for those collected in 2007 and 2008 in the same region (Matsuno et al., 2011), the plankton stocks in 2017 are considered to be an ordinary year.

While under these conditions, the four common interactions observed for both years (Table 1) are considered to be the strong interactions that characterize the plankton food web in this region. Among these four interactions, strong positive interaction between salinity and NO_x corresponds with that the high nutrient levels of the saline Anadyr Current (Danielson et al., 2017; Sigler et al., 2017). Negative interaction between temperature and NH₄ indicates that NH₄ is also high for the cold Anadyr Current. Since NH₄ is a product of decomposition and is high for the lower layer in this region (Brown et al., 2015), NH₄ may have a negative interaction with fresh phytoplankton. Phytoplankton abundance was high around the Bering Strait, which is characterized by the fast current in this region (Abe et al., 2019). Such high current velocity is not conducive to the presence of large-sized jellyfishes (De Robertis and Taylor, 2014). Thus, negative interaction may be detected between Phyto and Jelly (Table 1). From these viewpoints, the four common interactions observed in both years may be related to the regional topography and the water masses and are considered to be fundamental interactions of the planktonic food web in the northern Bering Sea.

Among interactions with opposing patterns between years, it is remarkable that salinity showed strong positive interaction with Phyto in 2017, while strong negative interaction was seen for 2018 (Table 1). As mentioned above, salinity had a strong positive interaction with nutrient (NO_x) levels in both years (Table 1). Thus, in 2018, while nutrient levels were high in the high saline region, Phyto levels were low for the region. For spring bloom in 2018, because of the early ice retreat, no ice-edge bloom and only a small-magnitude open-water bloom was reported (Duffy-Anderson et al., 2019). This relationship between ice and phytoplankton blooming is consistent with the Oscillating Control Hypothesis (OCH) reported for the southeastern Bering Sea shelf (Hunt et al., 2002, 2011). Observations of Meso in 2018 (the dominance of small-sized copepods during the late spring phytoplankton bloom in the warm year) may also reflect OCH (Duffy-Anderson et al., 2019). The low production and paucity of interactions within the planktonic food web in 2018 (Fig. 4) may have induced the failure of material and energy transfer to the higher trophic level. Since a low ice coverage area was also reported for the winter of 2018–2019 (Duffy-Anderson et al., 2019), if similar hydrography and ice conditions continue for successive years, serious effects may be inevitable for the marine ecosystem in the northern Bering Sea.

As the alternative possible forces in the marine ecosystem, while this study did not quantify the higher trophic levels, add to the bottom-up controls focusing in this study, the factors of top-down control should be considered. Based on the acoustic surveys, standing stocks of the age-zero Arctic cod in 2017 is reported to be 5–16 times greater than those in 2012–2013 (Huntington et al., 2020). From surface trawl surveys, the catch per unit effort for juvenile pink salmon is reported to be two times

greater in 2017 than the previous years (Huntington et al., 2020). Based on the bottom trawl surveys, because of the absence of cold pool (near-bottom shelf waters cooler than 2 °C, located south of the Bering Strait) which act as a thermal barrier that prevents north-wards migration of subarctic groundfish, increased biomass of walleye pollock, Pacific cod and northern rock sole are reported for the northern Bering Sea in 2017 (Stevenson and Lauth, 2019). Thus, all this information on standing stocks of fishes (both pelagic and benthic and juvenile to adults) indicates an increase of stocks in the northern Bering Sea. In this study, while we considered only for bottom-up control interactions within the lower trophic levels, the effects of top-down controls by higher-trophic fishes may be a possible cause of low biomasses of Meso, Macro and Jelly in 2018 (Fig. 3).

5. Conclusions

Interactions between environmental parameters and various plankton stocks in the northern Bering Sea were evaluated and compared for the two successive years (2017 and 2018). In this study, there were four common interactions observed in both years, while three interactions were opposite in direction between the two years. The four common interactions are considered to be fundamental within the planktonic food web in this region, while the latter three interactions are variable with yearly differences in ice coverage and ice retreat timing. The low ice coverage and early ice retreat were reported not only in the 2017–2018 winter but also for the 2018–2019 winter. If such ice conditions continue for more years, material and energy transport within the planktonic food web may be diminished, causing a serious effect on the higher trophic level.

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