



## Yearly comparison of the planktonic chaetognath community in the Chukchi Sea in the summers of 1991 and 2007



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### ABSTRACT

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

### 1. Introduction

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

Chaetognaths are reported to have the second largest zooplankton biomass after copepods worldwide (Terazaki, 1998). Chaetognaths feed

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

In this study, we made a yearly comparison of the summer chaetognath community on the Chukchi Sea shelf region between two years, 1991 and 2007. These years correspond to before (1991) and after (2007) the onset of large-scale ice reduction in summer (Walsh, 2013).

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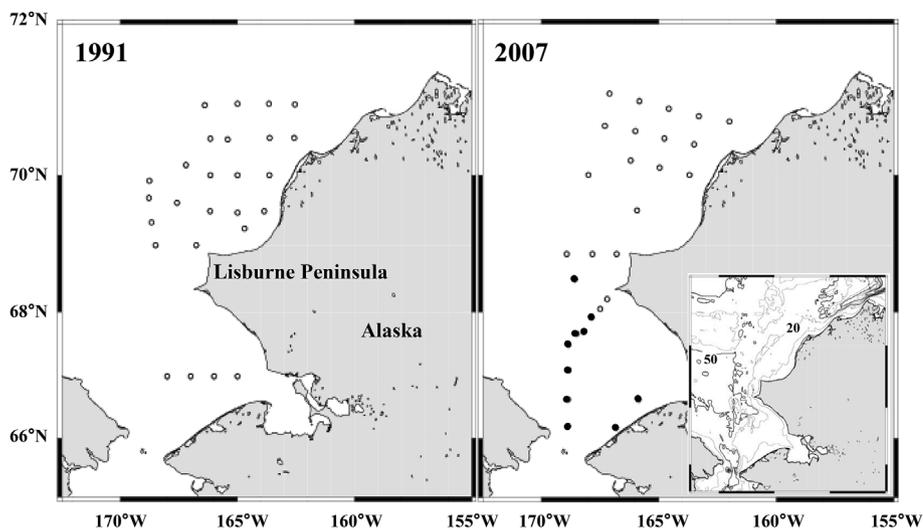


Fig. 1. Locations of sampling stations in the Chukchi Sea during 24–31 July 1991 (left) and 5–13 August 2007 (right). For reference, depth contours (20 and 50 m) are shown for the inset panel at the lower-right corner. Open circles: stations with only *Parasagitta elegans*. Solid circles: stations with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

The transportation of Pacific water in 2007 is reported to be the largest on record (Woodgate et al., 2010). We quantified the chaetognath abundance, biomass, body size, population structure and feeding impact in both years (1991 and 2007) and evaluated the effects of environmental changes on the chaetognath community.

## 2. Materials and methods

### 2.1. Field sampling

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

### 2.2. Sample analysis

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

Chaetognaths in the remaining half aliquots were sorted and identified to species under a stereomicroscope. The total lengths (TL, mm), from the top of the head to the end of the body without the caudal fin, of the dominant chaetognaths *P. elegans* and *E. hamata* were measured by callipers for large specimens ( $TL \geq 10 \text{ mm}$ ) or an eye-piece micrometer for small specimens ( $TL < 10 \text{ mm}$ ) to a precision of 0.1 mm. Based on gonadal maturation, *P. elegans* was classified into five stages:

juvenile and stages I, II, III, and IV (Thomson, 1947; Terazaki and Miller, 1986; Johnson and Terazaki, 2003). *E. hamata* was classified into eight stages: juvenile and stages I–VII (Kosobokova and Isachenko, 2017). Dry mass (DM,  $\mu\text{g ind.}^{-1}$ ) and biomass were calculated from the TL using the following equations:

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

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

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

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

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

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

where T indicates the integrated mean temperature of the sampling depths ( $^{\circ}\text{C}$ ). The feeding impact (no. of prey  $\text{m}^{-3} \text{ day}^{-1}$ ) was calculated by multiplying FR and *P. elegans* abundance ( $\text{ind. m}^{-3}$ ). By applying the calanoid copepod abundance data from the same zooplankton samples (Matsuno et al., 2011), the daily feeding impact of *P. elegans* ( $\% \text{ day}^{-1}$ ) was also calculated.

### 2.3. Statistical analysis

A cohort analysis was made of *P. elegans* TL data with the aid of Microsoft Excel Solver (Aizawa and Takiguchi, 1999). Because of the low abundance of *E. hamata*, no cohort analysis was made of this species. Yearly differences in environmental parameters (temperature, salinity), zooplankton (abundance, biomass), copepods (abundance), chaetognaths (abundance, biomass, mean TL and population structure) were tested by *U* test. To evaluate the factors governing chaetognath (*P. elegans*) abundance, a structural equation modelling (SEM) analysis was made for each year. For the SEM analysis, we analysed the correlations between *P. elegans* abundance and geographic parameters (latitude, longitude, depth), environmental parameters (integrated mean temperature and salinity) or biological parameters (abundances of small copepods, large copepods and Pacific copepods). Pacific copepods were

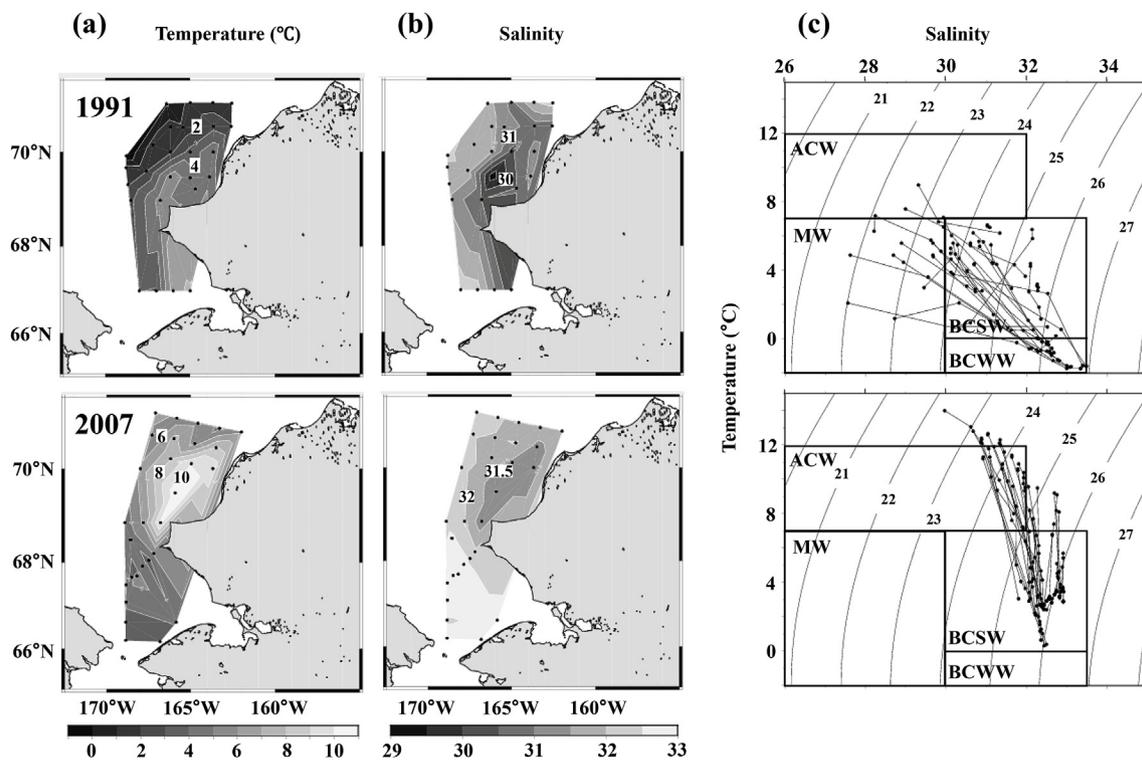


Fig. 2. Horizontal distributions of integrated mean temperature (a) and salinity (b), and the T-S diagram at each station (c) in the Chukchi Sea during 24–31 July 1991 (upper) and 5–13 August 2007 (lower). For the T-S diagram, the data at every 10 m (0, 10, 20, 30, 40 and 50 m) are connected with lines.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

defined as the following: *Neocalanus cristatus*, *N. flemingeri*, *N. plumchrus*, *Eucalanus bungii* and *Metridia pacifica*. *Calanus glacialis* and *C. hyperboreus* were considered large copepods. Small copepods included the remaining species, mainly *Pseudocalanus* spp. All these copepod data are from Matsuno et al. (2011).

### 3. Results

#### 3.1. Hydrography

In 1991, the integrated mean temperature and salinity ranged from 0.9 to 7.2 °C and 29.2 to 32.3, respectively (Fig. 2a and b). High temperature with less saline water was seen along the Alaskan coast. In 2007, the integrated mean temperature was 3.1–10.6 °C, and the salinity was 31.1–32.9. The yearly comparisons revealed that 2007 was characterised by higher temperatures and salinities than 1991. The plotted positions on the T-S diagram also varied greatly by year. Thus, the surface water was mainly composed of meltwater (MW) in 1991 and was dominated by the Alaskan Coastal Water (ACW) in 2007 (Fig. 2c). The bottom water was composed of the Bering-Chukchi Winter Water (BCWW) in 1991 and was dominated by the Bering-Chukchi Summer Water (BCSW) in 2007.

#### 3.2. Chaetognath abundance and biomass

In 1991, the chaetognath abundance was 177–1952 ind. m<sup>-2</sup> at the sampled stations (mean: 818 ind. m<sup>-2</sup>) and was high north of the Lisburne Peninsula (Fig. 3a). The biomass was 30.9–451.0 mg DM m<sup>-2</sup> (mean: 160.8 mg DM m<sup>-2</sup>) and was also high north of the Lisburne Peninsula (Fig. 3b). In 2007, the chaetognath abundance was 0–2491 ind. m<sup>-2</sup> (mean: 474 ind. m<sup>-2</sup>) and was high south of the Lisburne Peninsula. Biomass ranged from 0 to 388.5 mg DM m<sup>-2</sup> (mean: 78.6 mg DM m<sup>-2</sup>) and was also high south of the Lisburne Peninsula. Within the

chaetognath community, *P. elegans* was predominant in both years, comprising 100% (1991) or 95.5% (2007) of the cumulative catch. *E. hanata* only occurred south of the Lisburne Peninsula in 2007 to a limited extent (6–65 ind. m<sup>-2</sup> or 4.6–241.0 mg DM m<sup>-2</sup>) (Fig. 1).

#### 3.3. Total length and population structure

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

In 1991, the TL of *P. elegans* ranged from 1.0 to 26.3 mm (Fig. 4). The TLs of each stage 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, 16.1–25.9 mm. The TL histogram based on the cumulative data for the whole station clearly separated into two cohorts. The mean TL of the small cohort was 4.1 mm and was mainly composed of Juveniles, and the mean TL of the large cohort was 15.4 mm and composed of Stage I.

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

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

For *P. elegans*, a gut containing food items was seen in 34 specimens in 1991 and 47 specimens in 2007 (Table 1). All specimens contained one food item and no specimen had multiple prey items. For most of the gut contents, species identification was difficult because of digestion.

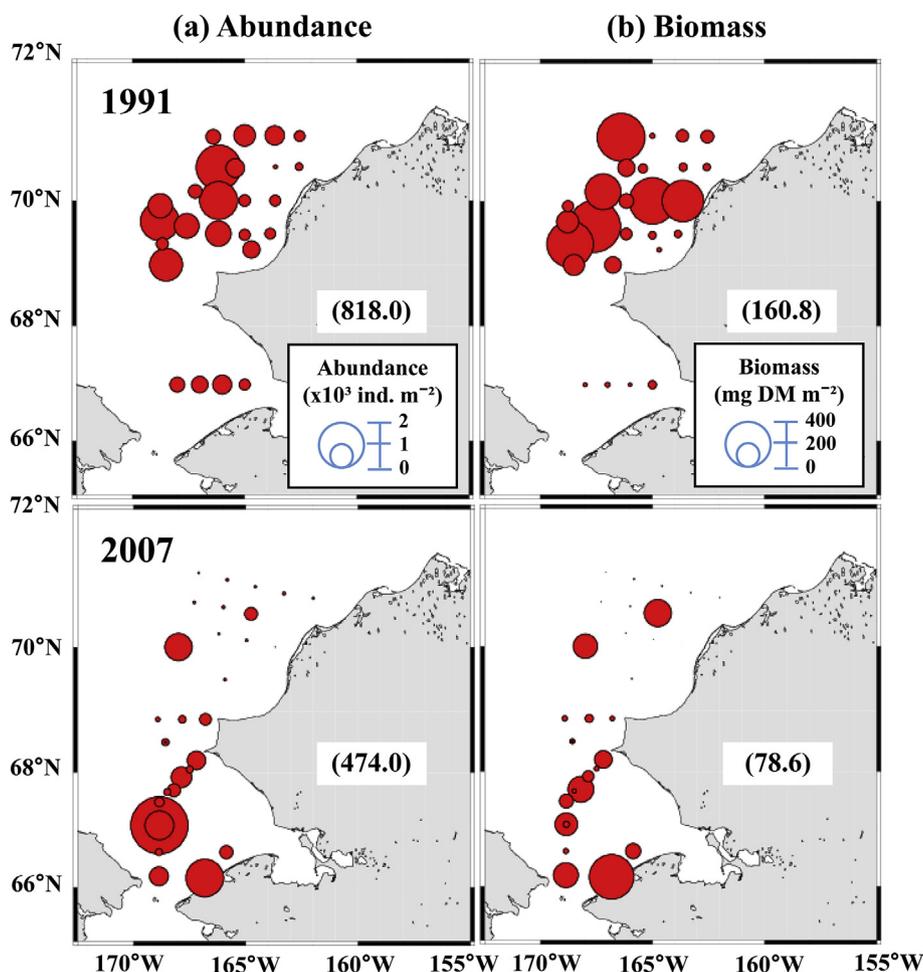


Fig. 3. Horizontal distributions of the chaetognath *Parasagitta elegans* abundance (a) and biomass (b) at each station in the Chukchi Sea during 24–31 July 1991 (upper) and 5–13 August 2007 (lower). Values in parentheses indicate mean abundance (ind. m<sup>-2</sup>) or biomass (mg DM m<sup>-2</sup>).

Species identification was not possible for 88.2% (1991) or 83.0% (2007) of the food items. Despite such limitations, the copepods *Calanus* sp., *Pseudocalanus* spp., *Pseudocalanus* spp. C2, *Pseudocalanus* spp. C5F, *Pseudocalanus* spp. C6F, *Metridia pacifica* C4, *Centropages abdominalis*, and *Eurytemora herdomani* C6 were identified as food items. For the yearly differences, *Pseudocalanus* spp. dominated in 1991, while *E. herdomani* dominated and was only seen in 2007.

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

### 3.5. SEM analysis

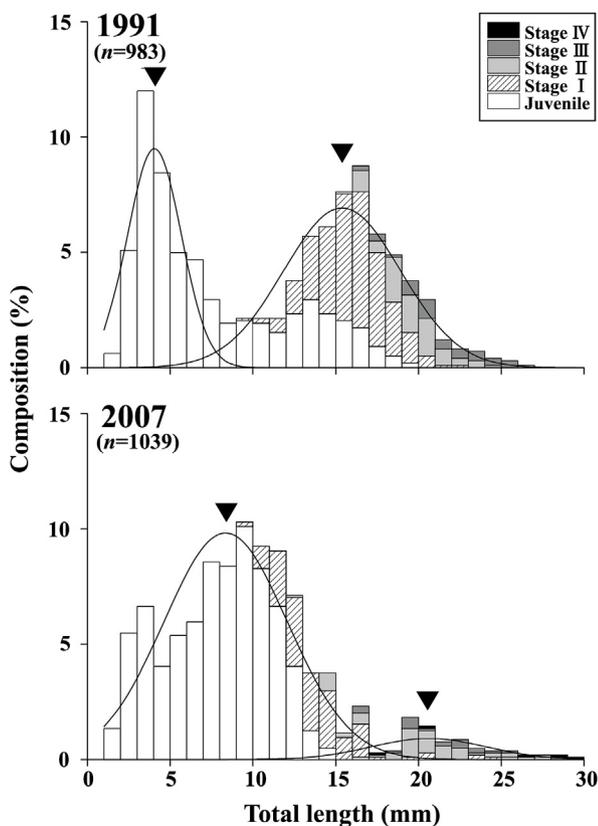
From the SEM analysis, the *P. elegans* abundance in 1991 showed that they were positively affected by the depth, integrated mean temperature, salinity and large-sized copepods and negatively affected by small copepods (Fig. 5). On the other hand, the *P. elegans* abundance in 2007 had fewer interactions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

## 4. Discussion

### 4.1. Methodological note

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

A diel feeding rhythm (nocturnal feeding) is also reported for *P. elegans* (Øresland, 1987; Terazaki, 1995). Bearing this in mind, the feeding intensity of *P. elegans* in this study is expected to be low under the midnight sun condition. This could be a possible cause of the low NPC of this study (0.035–0.045) compared with the reported values for *P. elegans* (0.4–0.9; Øresland, 1987; Tönnesson and Tiselius, 2005). Thus, the midnight sun condition of this study may have the possibility of a near-bottom distribution and a low *P. elegans* feeding intensity. These facts may have resulted in the collection of few large-sized (Fig. 4) and few food-containing individuals (Table 1) of *P. elegans* in this study. While these shortcomings are present, information on



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

**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	–	6.4
Unidentified organisms	88.2	83.0
Number of individual food containing ( $n$ )	34	47
Number of total individual ( $n$ )	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

species occurring as prey of *P. elegans* are valuable. Within them, copepods *C. abdominalis* and *E. herdomani* are the first record as prey for *P. elegans* (cf. Terazaki, 1998). Since both species are categorized as neritic species (Brodsky, 1967), it is expected that they would be included in the shallow depth region (< 50 m) of this study (Fig. 1).

#### 4.2. Horizontal distribution of chaetognaths

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

Chaetognaths are treated as water mass indicator species (cf. Pierrot-Bults, 2008). The surface and bottom water masses throughout the study area in 2007 were dominated by the ACW and BCSW, respectively (Fig. 2c). While the whole area was covered by the same water masses (ACW and BCSW), horizontal gradients of *E. hamata* distribution and a high abundance of *P. elegans* south of the Lisburne Peninsula area were prominent. The amount of Pacific water transported through the Bering Strait was reported to be highest in 2007 (Woodgate et al., 2010). These facts suggest that the amounts of transported chaetognaths originating in the Pacific were also high in 2007. In the Chukchi Sea, the dominant pelagic fish is age-0 Arctic cod (*Boreogadus saida*) (De Robertis et al., 2017). Chaetognaths are reported to be prey of Arctic cod and composed 1.2–8.7% in weight of prey (Buckley and Whitehouse, 2017). Through northward transport of the Pacific chaetognaths, they may suffer such high predation pressure by Arctic cod. It may be a possible cause of the low abundance of chaetognaths in the north of Lisburne Peninsula in 2007.

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

On the other hand, because of the great regional variability in environmental parameters in 1991 (Fig. 2), the horizontal distribution of chaetognaths may well explain the geographical, environmental and biological parameters using SEM analysis (Fig. 5). In 1991, few effects of the transportation of the water mass from the Pacific showed a stable chaetognath community in this region. Within the copepods (small copepods, large copepods and Pacific copepods), only small copepods had correlations with chaetognaths for both years (Fig. 5). A strong negative correlation in 1991 suggests that a high predation impact of *P. elegans* on small copepods was the cause of the stable condition in this region.

As an alternative explanation of the horizontal distribution of *P.*

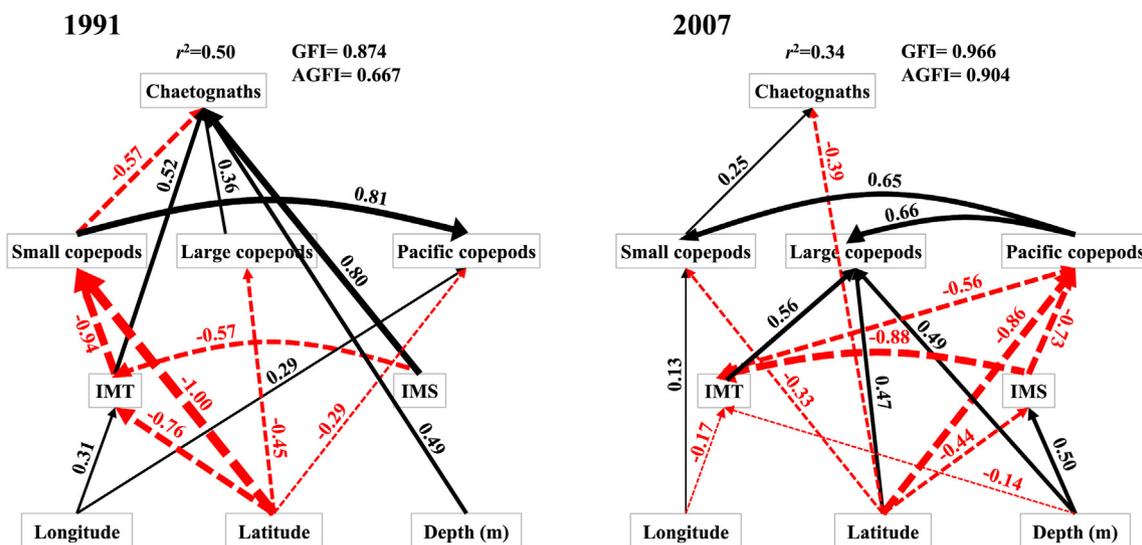


Fig. 5. Results of the structural equation model (SEM) for the chaetognath *Parasagitta elegans* abundances in the Chukchi Sea during 24–31 July 1991 (left) and 5–13 August 2007 (right). The values along the pathways represent standardised path coefficient values. Arrows with solid or dashed lines indicate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

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

### 4.3. Year-to-year changes in chaetognaths

The yearly environmental, biological and chaetognath community differences between 1991 and 2007 are summarised in Table 2. Both temperature and salinity were higher in 2007 (Fig. 2c). While the total zooplankton abundance and biomass did not vary with the year, the

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 ± 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 ± 2.0	< 5.8 ± 2.2	**
salinity	–	31.2 ± 0.8	< 32.1 ± 0.5	0.5
Zooplankton abundance	10 <sup>3</sup> ind. m <sup>-2</sup>	67.3 ± 57.1	71.1 ± 57.7	NS
biomass	g WM m <sup>-2</sup>	37.7 ± 26.6	42.8 ± 60.0	NS
Copepods abundance	10 <sup>3</sup> ind. m <sup>-2</sup>	13.0 ± 13.0	< 33.7 ± 37.2	*
Chaetognaths abundance	ind. m <sup>-2</sup>	818.0 ± 442.6	> 474.0 ± 551.2	**
biomass	mg DM m <sup>-2</sup>	160.8 ± 137.2	> 78.6 ± 97.1	**
mean body size	mm	11.5 ± 6.2	> 9.8 ± 5.0	**
maturation stage	–	1.5 ± 0.8	> 1.3 ± 0.7	**

copepod abundance was greater in 2007 (Table 2). This discrepancy is due to differences in the taxonomic composition of the zooplankton community with barnacle larvae dominating in 1991 (Matsuno et al., 2011).

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

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

For the widespread chaetognath *P. elegans*, regional differences in reproduction timing, life cycle and generation length are well-known (cf. Terazaki, 1998). For instance, the generation length is two years in the Arctic Ocean and one year at lower latitudes (Dunbar, 1962; Pierrot-Bults, 2008). At the high latitudes of the Arctic Ocean, the generation length is extended to three years (Grigor et al., 2014). In contrast, two generations in one year have been reported for warm low-latitude oceans (Zo, 1973). While the Chukchi and Bering seas are connected to each other, their temperatures and faunas are notably different (Pisareva et al., 2015). These facts suggest that the reproduction and life cycle timings of *P. elegans* may vary between the two oceans. Compared with 1991, the amount of transported Pacific water through Bering Strait in 2007 is known to be the highest on record (Woodgate et al., 2010). These facts suggest that the dominant chaetognaths south of the Lisburne Peninsula in 2007 may also be a transported expatriate community from the Bering Sea. Thus, different

life-cycle timings of *P. elegans* between the two oceans may be considered to provide yearly differences in body-size distribution between 1991 and 2007 (Fig. 4). Differences in body-size frequency may induce the yearly differences in the biomass and mean maturation stage observed in this study (Table 2).

## 5. Conclusions

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

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.polar.2018.11.011>.

## References

- Aizawa, Y., Takiguchi, N., 1999. Consideration of the methods for estimating the age-composition from the length frequency data with MS Excel. *Bull. Jpn. Soc. Fish. Oceanogr.* 63, 205–214 (in Japanese with English abstract).
- Brodsky, K.A., 1967. Calanoida of the Far Eastern Seas and Polar Basin of the USSR. Israel Program for Scientific Translations, Jerusalem.
- Buckley, T.W., Whitehouse, G.A., 2017. Variation in the diet of arctic cod (*Boreogadus saida*) in the pacific arctic and Bering sea. *Environ. Biol. Fish.* 100, 421–442.
- Cartes, J.E., 1998. Dynamics of the bathyal Benthic Boundary Layer in the northwestern Mediterranean: depth and temporal variations in macrofaunal– megafaunal communities and their possible connections within deep-sea trophic webs. *Oceanogr.* 41, 111–139.
- Conway, D.V.P., Williams, R., 1986. Seasonal population structure, vertical distribution and migration of the chaetognath *Sagitta elegans* in the Celtic Sea. *Mar. Biol.* 93, 377–387.
- Danielson, S.L., Eisner, L., Ladd, C., Mordy, C., Sousa, L., Weingartner, T.J., 2017. A comparison between late summer 2012 and 2013 water masses, macronutrients, and phytoplankton standing crops in the northern Bering and Chukchi Seas. *Deep-Sea Res. II* 135, 7–26.
- De Robertis, A., Taylor, K., Wilson, C.D., Farley, E.V., 2017. Abundance and distribution of arctic cod (*Boreogadus saida*) and other pelagic fishes over the U.S. Continental shelf of the northern bering and Chukchi seas. *Deep-Sea Res. II* 135, 51–65.
- Dunbar, M.J., 1962. The life cycle of *Sagitta elegans* in arctic and subarctic seas, and the modifying effects of hydrographic differences in the environment. *J. Mar. Res.* 20, 76–91.
- Eisner, L., Hillgruber, N., Martinson, E., Maselko, J., 2013. Pelagic fish and zooplankton species assemblages in relation to water mass characteristics in the northern Bering and southeast Chukchi seas. *Polar Biol.* 36, 87–113.
- Ershova, E.A., Hopcroft, R.R., Kosobokova, K.N., 2015. Inter-annual variability of summer mesozooplankton communities of the western Chukchi Sea: 2004–2012. *Polar Biol.* 38, 1461–1481.
- Fujiwara, A., Hirawake, T., Suzuki, K., Imai, I., Saitoh, S.I., 2014. Timing of sea ice retreat can alter phytoplankton community structure in the western Arctic Ocean. *Biogeosciences* 11, 1705–1716.
- Gray, B.P., Norcross, B.L., Blanchard, A.L., Beaudreau, A.H., Seitz, A.C., 2016. Variability in the summer diets of juvenile polar cod (*Boreogadus saida*) in the northeastern Chukchi and western Beaufort Seas. *Polar Biol.* 39, 1069–1080.
- Grebmeier, J.M., 2012. Shifting patterns of life in the pacific arctic and sub-arctic seas. *Annu. Rev. Mar. Sci.* 4, 63–78.
- Grigor, J.J., Søreide, J.E., Varpe, Ø., 2014. Seasonal ecology and life-history strategy of the high-latitude predatory zooplankton *Parasagitta elegans*. *Mar. Ecol. Prog. Ser.* 499, 77–88.
- Grigor, J.J., Schmid, M.S., Fortier, L., 2017. Growth and reproduction of the chaetognaths *Eukrohnia hamata* and *Parasagitta elegans* in the Canadian Arctic Ocean: capital breeding versus income breeding. *J. Plankton Res.* 39, 910–929.
- Hopcroft, R.R., Kosobokova, K.N., Pinchuk, A.I., 2010. Zooplankton community patterns in the Chukchi Sea during summer 2004. *Deep-Sea Res. II* 57, 27–39.
- Johnson, T.B., Terazaki, M., 2003. Species composition and depth distribution of chaetognaths in a Kuroshio warm-core ring and Oyashio water. *J. Plankton Res.* 25, 1279–1289.
- King, K.R., 1979. The life history and vertical distribution of the chaetognath, *Sagitta elegans*, in Dabob Bay, Washington. *J. Plankton Res.* 1, 153–167.
- Kosobokova, K.N., Hanssen, H., Hirche, H.J., Knickmeier, K., 1998. Composition and distribution of zooplankton in the Laptev Sea and adjacent Nansen basin during summer, 1993. *Polar Biol.* 19, 63–73.
- Kosobokova, K.N., Hirche, H.J., 2000. Zooplankton distribution across the Lomonosov Ridge, Arctic Ocean: species inventory, biomass and vertical structure. *Deep-Sea Res. I* 47, 2029–2060.
- Kosobokova, K.N., Isachenko, A.I., 2017. The gonad maturation and size structure of the population of abundant planktonic predator *Eukrohnia hamata* (Möbius, 1875) (Chaetognatha) in the Eurasian basin of the Arctic Ocean in summer. *Russ. J. Mar. Biol.* 43, 25–33.
- Matsumoto, Y., 2008. Life Cycle and Production of Chaetognath *Eukrohnia Hamata* in the Oyashio Region, Western North Pacific (Master Thesis). Hokkaido University, Hokkaido (in Japanese).
- Matsuno, K., Hirawake, T., Yamaguchi, A., Imai, I., 2011. Year-to-year changes of the mesozooplankton community in the Chukchi Sea during summers of 1991, 1992 and 2007. *Polar Biol.* 34, 1349–1360 2008.
- McLaren, I.A., 1963. Effects of temperature on the growth of zooplankton, and the adaptive value of vertical migration. *J. Fish. Res. Board Can.* 20, 685–727.
- Motoda, S., 1957. North Pacific standard plankton net. *Inform. Bull. Plankton Japan* 4, 13–15.
- Motoda, S., 1959. Devices of simple plankton apparatus. *Mem. Fac. Fish. Hokkaido Univ.* 7, 73–94.
- Nagasawa, S., Marumo, R., 1972. Feeding of a pelagic chaetognath, *Sagitta nageae* alvarinho in suruga bay, central Japan. *J. Oceanogr. Soc. Jpn.* 28, 181–186.
- Nakamura, A., Matsuno, K., Abe, Y., Shimada, H., Yamaguchi, A., 2017. Length-weight relationships and chemical composition of the dominant mesozooplankton taxa/species in the subarctic Pacific, with special reference to the effect of lipid accumulation in Copepoda. *Zool. Stud.* 56, 13. <https://doi.org/10.6620/ZS.2017.56-13>.
- Øresland, V., 1987. Feeding of the chaetognaths *Sagitta elegans* and *S. setosa* at different seasons in Gullmarsfjorden, Sweden. *Mar. Ecol. Prog. Ser.* 39, 69–79.
- Ozawa, M., Yamaguchi, A., Kitamura, M., 2004. Small scale distribution of chaetognaths at Shiribeshi Seamount in the northern Japan Sea; an analysis of video records of submersible remotely operated vehicle. *Bull. Fish. Sci. Hokkaido Univ.* 55, 145–150.
- Pearre Jr., S., 1981. Feeding by Chaetognatha: energy balance and importance of various components of the diet of *Sagitta elegans*. *Mar. Ecol. Prog. Ser.* 5, 45–54.
- Perovich, D.K., 2011. The changing Arctic sea ice cover. *Oceanography* 24, 162–173.
- Pierrot-Bults, A.C., 2008. A short note on the biogeographic patterns of the Chaetognatha fauna in the North Atlantic. *Deep-Sea Res. II* 55, 137–141.
- Pinchuk, A.I., Eisner, L.B., 2017. Spatial heterogeneity in zooplankton summer distribution in the eastern Chukchi Sea in 2012–2013 as a result of large-scale interactions of water masses. *Deep-Sea Res. II* 135, 27–39.
- Pisareva, M.N., Pickart, R.S., Spall, M.A., Nobre, C., Torres, D.J., Moore, G.W.K., Whitledge, T.E., 2015. Flow of pacific water in the western Chukchi Sea: results from the 2009 RUSALCA expedition. *Deep-Sea Res. I* 105, 53–73.
- Questel, J.M., Clarke, C., Hopcroft, R.R., 2013. Seasonal and interannual variation in the planktonic communities of the northeastern Chukchi Sea during the summer and early fall. *Continent. Shelf Res.* 67, 23–41.
- Sameoto, D.D., 1971. Life history, ecological production, and an empirical mathematical model of the population of *Sagitta elegans* in St. Margaret's Bay, Nova Scotia. *J. Fish. Res. Board Can.* 28, 971–985.
- Søreide, J.E., Leu, E., Berge, J., Graeve, M., Falk-Petersen, S., 2010. Timing of blooms, algal food quality and *Calanus glacialis* reproduction and growth in a changing Arctic. *Global Change Biol.* 16, 3154–3163.
- Terazaki, M., 1995. The role of carnivorous zooplankton, particularly chaetognaths in ocean flux. In: Sakai, H., Nozaki, Y. (Eds.), *Biogeochemical Processes and Ocean Flux*

- in Western Pacific. Terra Scientific Publishing Company, Tokyo, pp. 319–330.
- Terazaki, M., 1998. Life history and distribution, seasonal variability and feeding of the pelagic chaetognath *Sagitta elegans* in the subarctic Pacific: a review. *Plankton Biol. Ecol.* 45, 1–17.
- Terazaki, M., Miller, C.B., 1986. Life history and vertical distribution of pelagic chaetognaths at Ocean Station P in the subarctic Pacific. *Deep-Sea Res. A* 33, 323–337.
- Thomson, J.M., 1947. The chaetognaths of southern Australia. *Com. Sci. Ind. Res. Bull.* 222, 1–43.
- Tönnesson, K., Tiselius, P., 2005. Diet of the chaetognaths *Sagitta setosa* and *S. elegans* in relation to prey abundance and vertical distribution. *Mar. Ecol. Prog. Ser.* 289, 177–190.
- Walsh, J.E., 2013. Melting ice: what is happening to Arctic sea ice, and what does it mean for us? *Oceanography* 26, 171–181.
- Woodgate, R.A., Weingartner, T., Lindsay, R., 2010. The 2007 Bering Strait oceanic heat flux and anomalous Arctic sea-ice retreat. *Geophys. Res. Lett.* 37, L01602. <https://doi.org/10.1029/2009GL041621>.
- Zo, Z., 1973. Breeding and growth of the chaetognath *Sagitta elegans* in bedford basin. *Limnol. Oceanogr.* 18, 750–756.