Article

Dynamics of *Calanus* Copepodite Structure during Little Auks' Breeding Seasons in Two Different Svalbard Locations

Kaja Balazy *[ID], **Emilia Trudnowska**[ID] and **Katarzyna Błachowiak-Samołyk**

Institute of Oceanology, Polish Academy of Sciences, Powstańców Warszawy 55, 81-712 Sopot, Poland
* Correspondence: kaja@iopan.pl; Tel.: +48-58-7311696

check for updates

Abstract: Populations dynamics of key zooplankton species in the European Arctic, *Calanus finmarchicus* and *Calanus glacialis* (hereafter defined as *Calanus*) may be sensitive to climate changes, which in turn is of great importance for higher trophic levels. The aim of this study was to investigate the complete copepodite structure and dynamics of *Calanus* populations in terms of body size, phenology and their relative role in the zooplankton community over time in different hydrographic conditions (two fjords on the West Spitsbergen Shelf, cold Hornsund vs. warm Kongsfjorden), from the perspective of their planktivorous predator, the little auk. High-resolution zooplankton measurements (taken by nets and a laser optical plankton counter) were adapted to the timing of bird's breeding in the 2015 and 2016 summer seasons, and to their maximal diving depth (≤50 m). In Hornsund, the share of the *Calanus* in zooplankton community was greater and the copepodite structure was progressively older over time, matching the little auks timing. The importance of *Calanus* was much lower in Kongsfjorden, as represented mainly by younger copepodites, presumably due to the Atlantic water advections, thus making this area a less favourable feeding ground. Our results highlight the need for further studies on the match/mismatch between *Calanus* and little auks, because the observed trend of altered age structure towards a domination of young copepodites and the body size reduction of *Calanus* associated with higher seawater temperatures may result in insufficient food availability for these seabirds in the future.

Keywords: population dynamics; size; match-mismatch; Spitsbergen; laser optical plankton counter

1. Introduction

Calanus finmarchicus and *Calanus glacialis* (hereafter *Calanus*) co-exist and dominate the mesozooplankton biomass in the shelf waters of the Arctic Ocean [1–3]. Originally, both species have different centers of distribution and thus are adapted to different environmental conditions and consequently adopt different life-history strategies [4–7]. As dynamic changes in the environmental conditions and in timing of primary production in the Arctic [8] cause high variability in the development rate and length of life cycles of the *Calanus* species [9], comprehensive phenological studies of these copepods are essential, especially in the context of their availability to planktivores in the warming Arctic. The important role of *Calanus* spp. in marine ecosystem functioning is based on the transfer of omega-3 fatty acids (long-chain PUFAs produced by marine algae), which are crucial for the growth and reproduction of all marine organisms [10]. *Calanus* spp. are full of lipids (up to 50–70% in dry mass) [11–13], and this makes them extremely nutritious for planktivores. Until recently, the amount of lipids was suggested to be species-specific, with a higher lipid content attributed to *C. glacialis* compared to the smaller *C. finmarchicus* [4,5,13]. This assumption emphasized the different role of these species in the Arctic ecosystem. However, in most of the studies the identification between these

two morphologically very similar species was based on their size [13–15], while according to recent molecular studies the size ranges of *C. glacialis* and *C. finmarchicus* overlap and are generally much broader than previously assumed [16–20]. Therefore, the problem with a correct separation of these species could lead to substantial confusion dealing with their life history, population dynamics and ecological roles. Because the lipid content was found to depend on body size rather than species, the analysis of the *Calanus* spp. size seems to be more appropriate to understanding the process of energy transfer from *Calanus* to higher trophic levels [20].

The individual size of *Calanus* spp. is tightly coupled with the ambient seawater temperature, with smaller individuals observed in warmer seawater conditions [16,21,22]. Temperature increase affects not only intra-species size variability but leads also to alteration of the zooplankton community size structure, which is considered to be more important than shifts in biomass [23,24]. The scenarios of pelagic food web modifications due to the increased seawater temperature indicate that smaller boreal species, due to faster reproduction, will have increasingly important roles in the higher latitudes [15,20,25]. A northward expansion of organisms, better adapted to warm water conditions, has already been observed [26–28]. Fluctuations in planktonic production may lead to a disturbance in interactions between predators and prey (match/mismatch) [29,30] and as a consequence may severely disrupt the functioning of the whole ecosystem [31–34]. However, new hypotheses have also emerged, suggesting that energy transfer to higher trophic levels may be more efficient than previously assumed, because of the accelerated zooplankton development [20]. Unfortunately, such promising scenarios may not apply to strictly specialized visual predators, actively selecting larger *Calanus* spp. individuals, such as the little auk [35,36], the keystone planktivorous seabird in the Arctic [37]. The little auk requires their prey to occur in high proportion in relation to other zooplankters in the seawater [14,37], because high abundances of small zooplankters may hinder the detection of their preferred large, energy-rich prey. The reproduction period of little auks is tightly matched in time with particular phase of *Calanus* development, because they actively select mainly the lipid-full fifth copepodite stage (CV) [38–43]. A recent study of *Calanus* spp. phenology in Greenland waters [44] showed that little auks select foraging grounds where availability of their main prey is matched in time with their high food demands. This might be especially important in Svalbard, where some of the world's largest colonies of these birds are located [45] and which is now threatened by the new climate state due to progressing Atlantification. Little auks are the main fertilizers of ornithogenic tundra and thus play an important role in the Arctic ecosystem [46]. Therefore, studies of the phenology of their main prey are important for better understanding threats for both marine and terrestrial ecosystems and their interactions.

Consequently, two main goals emerged in this study: (1) to test the size of zooplankton both on individual (*Calanus* copepodite stages) and community (abundance-weighted mean size) levels; and (2) to investigate dynamics of complete copepodite structure of *Calanus* in the context of food demand of the little auk during the summer chick rearing period in two different regions and summer seasons on the West Spitsbergen Shelf. We hypothesized that both the population dynamics of *Calanus* and the taxonomic composition of zooplankton vary significantly between more Atlantic and Arctic water dominated regions, which in turn provide different feeding conditions for planktivores.

2. Materials and Methods

2.1. Study Area

Research was conducted on the west coast of Spitsbergen in two fjords, representing different hydrographic regimes: Kongsfjorden, located in the north and Hornsund in the south (Figure 1). Hornsund is situated on the south-western tip of Spitsbergen and is influenced by the coastal Sørkapp Current, which carries less-saline, cold Arctic water [47,48]. Kongsfjorden is exposed to advection from the warmer Atlantic water of the West Spitsbergen Current (WSC) [48–50]. The two different currents are separated by a density gradient that forms the large frontal system along the West Spitsbergen

Shelf (WSS) [51]. Thus, Kongsfjorden receives twice as much Atlantic water than Hornsund, and this results in 1 °C higher water temperatures and 0.5 higher salinities compared to Hornsund [48]. However, in recent years, gradual warming has been observed in both fjords [48,52].
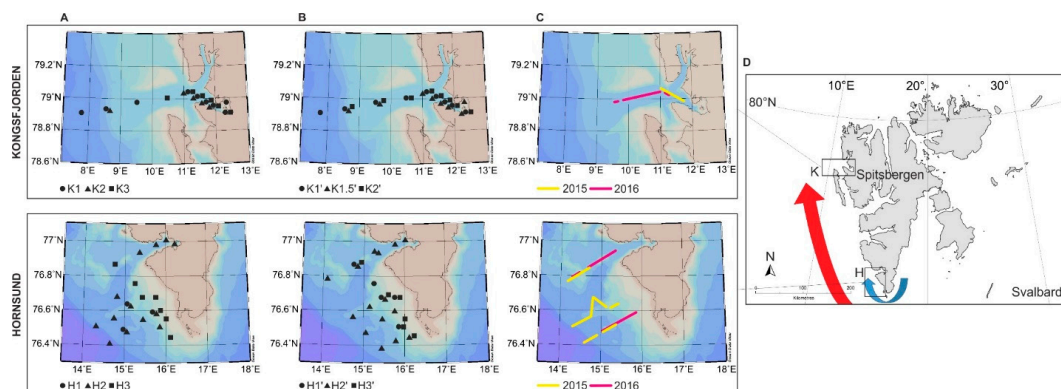

Figure 1. Zooplankton sampling stations in 2015 (**A**) and 2016 (**B**) from two fjords: Kongsfjorden (upper panel) and Hornsund (lower panel) located along the coast of Spitsbergen and sampled during three study periods each year (marked by various shapes of points). The sections of laser optical plankton counter (LOPC) surveys (**C**) are marked with yellow and pink lines. Map of the study area (**D**) with current patterns in the Spitsbergen region (simplified from Sakshaug et al. 2009).

2.2. Sampling Protocol

Zooplankton samples from the little auk foraging grounds were collected during two consecutive summer seasons (hereafter study season) of 2015 and 2016 (Figure 1 and Figure S1) in two study locations of cold Hornsund, and warm Kongsfjorden, both inside the fjords and in the adjacent areas located on the WSS (Figure 1). In Hornsund, samples were collected three times during each season, (hereafter study periods): three, 13, and seven samples in 2015 (hereafter respectively H1, H2, H3) and five, 15, and seven in 2016 (respectively H1′, H2′, H3′). In Kongsfjorden nine, five, and six samples were collected in 2015 (hereafter respectively K1, K2, K3) and nine, eight, and nine in 2016 (K1′, K1.5′, K2′). For exact sampling dates see Figure S1. In total, during 12 zooplankton sampling campaigns, 96 zooplankton samples were collected: 50 in the Hornsund area, and 46 in the Kongsfjorden area. Most sampling was performed directly from the R/V Oceania (IO PAN). Two sampling campaigns in the Kongsfjorden area (K1 and K2′) were performed on board of the R/V Lance (Norwegian Polar Institute), one on board of a Zodiac boat (K3 in 2015) and one in Hornsund on board the S/Y Magnus Zaremba (H3′ in 2016). Most of the samples (91) were collected using a WP2-type net (0.25 m^2 opening area) fitted with filtering gauze of 180 μm mesh size, which is best suited to catch all copepodite stages of *Calanus*. Five samples (K2) were collected using a WP2-type net with 60 μm mesh size. All zooplankton samples were collected from the mid-surface water layer (i.e., upper 50 m), which was arbitrarily chosen taking into consideration the little auk maximal diving depth of 50 m [53]. After collection, all samples were preserved in 4% formaldehyde solution in borax-buffered seawater and transported to laboratory for analysis.

2.3. Laboratory Analyses

Detailed laboratory analyses of each sample were performed according to a standard procedure, following the instructions given by Kwasniewski et al. [14]. First, zooplankters larger than 0.5 cm were removed from the sample, identified, and counted. Then, 2 mL subsamples were taken from each sample with a macropipette according to the sub-sampling method described by Harris et al. [54]. Subsamples were taken until at least 400 individuals were counted from a single sample. All organisms were identified to the lowest possible taxonomic level, typically species. Special focus was put on *Calanus* and their copepodite stages, which were identified according to criteria described by

Kwasniewski et al. [55]. The abbreviations (CI-AF) refer to six successive copepodite stages of *Calanus*, i.e., CI, CII, CIII, CIV and CV as the first five copepodite stages, and AF to adult females. After microscope analysis, the number of individuals in each sample was converted into abundance (ind. m^{-3}), basing on the volume of filtered water.

Due to the similar function of both species according to the trait-based approach [20] and difficulties in distinguishing them properly, for the purposes of this work *C. glacialis* and *C. finmarchicus* have been merged into one group, hereafter *Calanus*. However, the measurements of the prosome length of all copepodite stages of *Calanus* were performed for at least 30 individuals from each copepodite stage in the subsamples. To compare the prosome length of all the *Calanus* copepodite stages, 12,800 individuals were measured.

2.4. Temperature Measurements

Temperature data for comparison with the measurements of body size of *Calanus* and zooplankton community from net samples were obtained from 52 stations, (35 in Hornsund and 17 in Kongsfjorden) in two years of study by vertical profiles using a conductivity–temperature–depth sensor (CTD)). Measurements were first all binned into 1 m depth intervals, and then averaged over the upper 50 m water column for each station.

2.5. LOPC Measurements

To measure the size and concentrations of *Calanus*-type particles in different temperatures, the continuous oscillatory profiles, from the surface to 50 m depth, were performed with a conductivity–temperature–depth sensor (CTD; SBE 911plus, Seabird Electronics Inc., Washington, DC, USA) and a laser optical plankton counter (LOPC; Brooke Ocean Technology Ltd., Dartmouth, NS, Canada). The LOPC is an in-situ sensor that provides data on the abundance and size structure of a plankton community by measuring each particle passing through a sampling tunnel of a 49 cm^2 cross section. As the particle passes the sensor, the portion of blocked light is measured and recorded as a digital size and converted to the equivalent spherical diameter (ESD). The ESD is the diameter of a sphere that would represent the same cross-sectional area as the particle being measured with the use of a semi-empirical formula based on calibration with spheres of known diameters [56–58]. A *Calanus*-type group of particles, that involved only older life stages (app. CV), was selected basing on size (0.9–2.5 mm ESD) and transparency (attenuance index > 0.4) [59]. Then, the measurements (size + concentration of *Calanus*-type) were grouped according to a few seawater temperature ranges (<4 °C, 4–6 °C, and >6 °C) to calculate the 1d kernel density (R function geom_density) estimates of the dominating size in particular water temperatures.

2.6. Data Analyses

Multivariate nonparametric permutational ANOVA (PERMANOVA) [60] was used to test differences in: *Calanus* prosome length of individual copepodite stages; *Calanus* copepodite structure (CI-AF, stage index, and zooplankton species composition among fixed factors of regions and study periods. Prior to the analyses, abundance data were square-root-transformed [61]. The distribution of centroids representing particular samples was illustrated with a non-metric multi-dimensional scaling (nMDS) using Bray–Curtis similarities ordinations. The calculation of the Pseudo-F and *p* values was based on 999 permutations of the residuals under a reduced model [62]. To assess the magnitude of the spatial variation at each gradient, the estimated components of variation (ECV) as a percentage of the total variation were used. The relationship between seawater temperature and the *Calanus* prosome length and the mean size of zooplankton organisms was tested with the use of Pearson linear correlation. The *Calanus* stage index was calculated as a weighted mean on the basis of relative abundance of particular life stages, with each stage given values from 1 (CI) to 6 (AF) [63], where AF stage was represented by adult females. The mean size of zooplankton organisms in the sample was calculated as a weighted mean based on a local database with detailed measurements

made by the Svalbard fiords in the scope of the Dwarf project (Polish-Norwegian Research project no. Pol-Nor/201992/93/2014). To determine zooplankton community structure, relative abundance of species/taxa was used. For each study period, a median number of individuals of a given taxa was calculated. Taxa constituting more than 5% of total zooplankton abundance were distinguished; the rest were grouped into an "others" category. To compare the prosome length frequency distribution of a copepodite stage CV of *C. finmarchicus* and *C. glacialis*, the number of all CVs in the sample (ind. m^{-3}) was divided by the total number of measured individuals in the sample. To determine the relative abundance of measured individuals, each measurement of a given individual was multiplied by a factor: the abundance of CV (ind. m^{-3})/number of measured individuals. Measured individuals were classified into size classes every 0.05 mm.

3. Results

3.1. Size Response of Calanus and Mesozooplankton to Different Seawater Temperatures

The prosome length of *Calanus* copepodite stages based on comprehensive morphometrical analysis differed significantly between the two fjords in the case of all life stages (CI–CV), except for adults (AF) (Table 1). In general, the median prosome length of *Calanus* individuals was larger in Hornsund than in Kongsfjorden (Figure 2).

Table 1. Results of one-factor multivariate PERMANOVA for the prosome length of *Calanus* copepodite stages in Hornsund and Kongsfjorden. Bold means $p < 0.05$, df are degrees of freedom, MS represents means of squares, √ECV are square root of the estimated components of variance.

Copepodite Stage	Factor	df	MS	Pseudo-F	*p*	√ECV
CI	Fjord	1	1274.8	212.98	**0.001**	1.40
CII	Fjord	1	5180.9	560.51	**0.001**	2.43
CIII	Fjord	1	8748.4	1086.40	**0.001**	2.74
CIV	Fjord	1	5728.8	720.28	**0.001**	1.98
CV	Fjord	1	2277.5	237.43	**0.001**	1.43
AF	Fjord	1	1.2	0.22	0.630	−0.18

The prosome length of individual copepodite stages of *Calanus* significantly correlated with temperature in both fjords for CI-CV (Pearson correlation coefficient, R = −0.37, $p < 0.001$ (CI); R = −0.48, $p < 0.001$ (CII); R = −0.39, $p < 0.001$ (CIII); R = −0.38, $p < 0.001$ (CIV); R = −0.37, $p < 0.001$ (CV), Figure 3), and did not correlate for AF (Pearson correlation coefficient, R = 0.01, $p = 0.88$, Figure 3). Generally, a relatively large variation in the body size of each *Calanus* copepodite stage was observed for each temperature recorded, except for the highest values (>7 °C), at which only relatively small individuals were observed in Kongsfjorden.
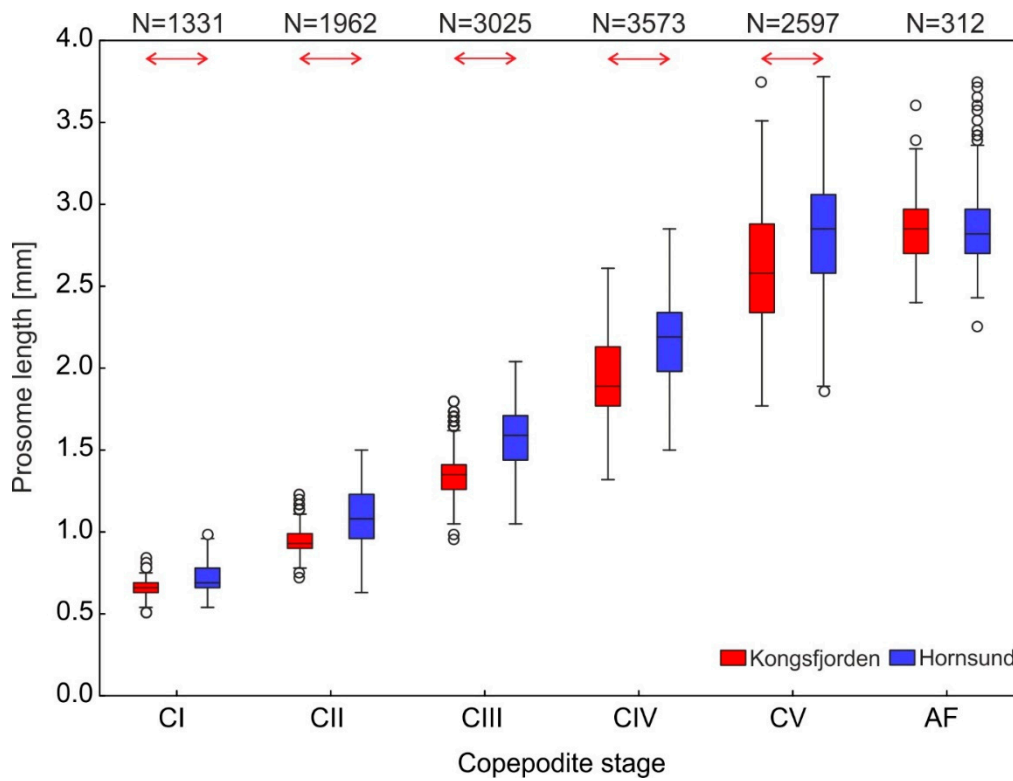
Figure 2. Prosome length of *Calanus* copepodite stages: CI–adult females (AF) in Kongsfjorden (red) and Hornsund (blue). Horizontal black lines in the boxes show the median, box represents percentiles, whiskers indicate ranges, dots represent values outside the range, red arrows show statistically significant size differences between two investigated fjords, N indicates number of measured individuals.
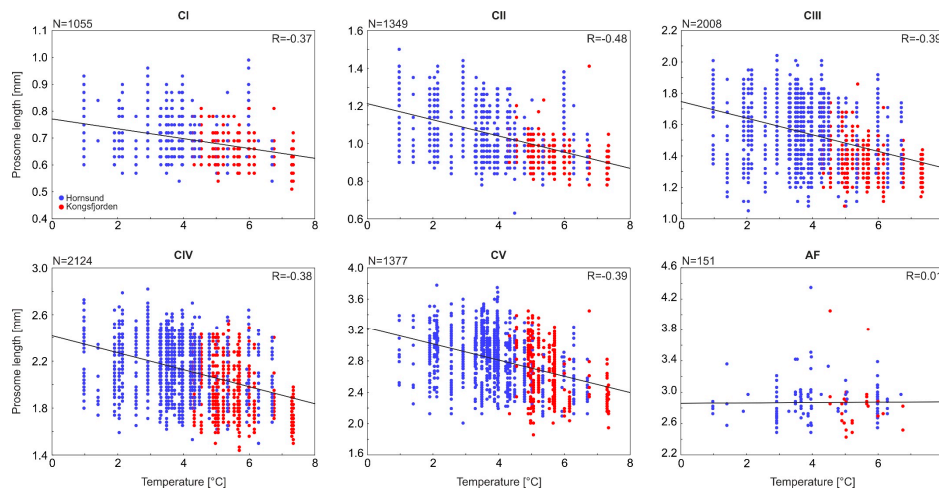

Figure 3. The relation between seawater temperature and prosome length of *Calanus* copepodite stages CI–AF. Dots represent individuals measured, blue in Hornsund and red in Kongsfjorden. Trendline is marked in black, N indicates the number of measured individuals, R indicates Pearson correlation coefficient.

Additionally, a significant negative correlation between seawater temperature and mean zooplankton body size was observed (Pearson's correlation R = −0.46; *p* = 0.001; Figure S2). Larger animals (>1200 μm) were observed at lower seawater temperatures (i.e., below 4 °C) in Hornsund, while smaller organisms were dominating mainly in warmer (4–7.5 °C) Kongsfjorden.

Moreover, according to the measurements of the automatic LOPC method of the *Calanus*-type particles, individual size of older life stages of *Calanus* (CIV and CV) also differed in relation to the seawater temperature (Figure 4). In Hornsund in both years the largest *Calanus*-type particles (c.a. 1.5 mm ESD) were observed in low temperatures (<4 °C), while the highest densities of smallest individuals (1.0–1.2 mm ESD) were noted at higher temperatures (>6 °C). In Kongsfjorden, the size range of older *Calanus* differed between two years, with larger size fraction dominating in 2015 (Figure 4).
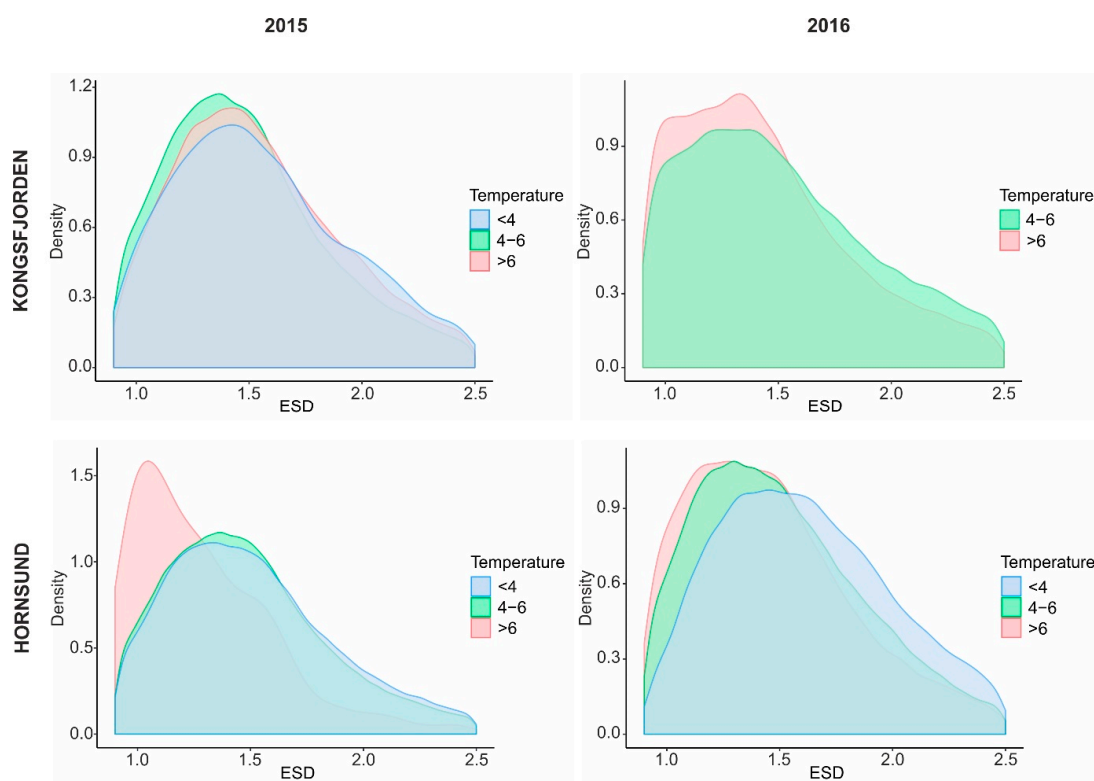
Figure 4. Size distribution of Calanus-type particles expressed as equivalent spherical diameter (ESD, mm) recorded by laser optical plankton counter (LOPC) in different temperature ranges in Kongsfjorden and Hornsund in 2015 and 2016.

3.2. Zooplankton Community Structure

The zooplankton community structure in Kongsfjorden was significantly different between the two years (PERMANOVA, MS = 6127.4, Pseudo-F = 16.13, p = 0.001) and among study periods in 2015 (PERMANOVA, MS = 1776.3, Pseudo-F = 5.22, p = 0.003) and in 2016 (PERMANOVA, MS = 2133.0, Pseudo-F = 4.49, p = 0.001). Because samples in K2 period of 2015 were collected with different net mesh size, they were excluded from the current analysis (see M and M for details). In 2015, *Calanus* was the most abundant taxon in K1, when it reached 47% of the total zooplankton abundance. Its percentage decreased over time reaching 25% in K3 (Figure 5). In 2016, the *Calanus* percentage was relatively low, and decreased from 12% in K1′ and K1.5′ to 5% in K2′ (Figure 5). The second numerous taxon, *Oithona similis* was more significant in 2015 (30% in K1 and 46% in K3) than in 2016 (20% throughout three study periods). The share of the Copepoda nauplii was higher (maximum in K1′) in 2016 than in 2015. Similarly as in Hornsund, the percentage of Bivalvia veligers were especially high in 2016 (17–26%) and very low in 2015 (≤5% in K3). Another important zooplankton component in Kongsfjorden was *Limacina helicina* with 16% to 31% contribution to the overall zooplankton abundances in 2016. The percentage of *Pseudocalanus* spp. was rather constant over time.
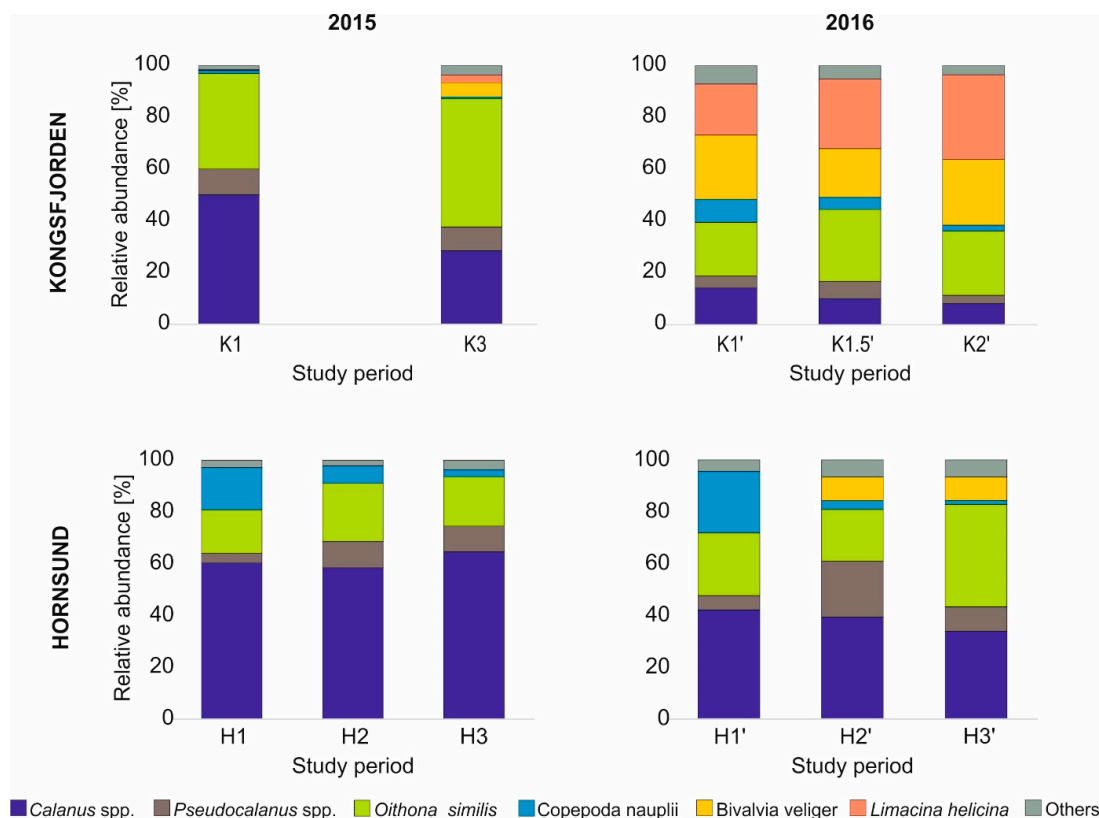
Figure 5. Zooplankton community structure in Kongsfjorden and Hornsund.

The zooplankton community structure in Hornsund also differed between the two years (PERMANOVA, MS = 3245.0, Pseudo-F = 5.83, p = 0.001) and between study periods (PERMANOVA, MS = 5222.6, Pseudo-F = 9.39, p = 0.001) of both years (PERMANOVA, MS = 1661.3, Pseudo-F = 2.98, p = 0.003). In both years, *Calanus* dominated the zooplankton community, constituting approx. 60% of total zooplankton abundance in all three study periods of 2015 and approximately 40% in 2016. The second most numerous taxon was *O. similis* with at least 20% of total zooplankton abundance throughout all the periods of both study seasons (Figure 5). Copepoda nauplii composed a significant percentage of total zooplankton abundance, especially in H1 and H1′ (20%). The contribution of *Pseudocalanus* spp. was in general the most important in H2 and H2′ study periods, while Bivalvia veligers comprised about 10% of all taxa in H2′ and H3′ in summer 2016.

3.3. Calanus Copepodite Structure

The copepodite structure of *Calanus* in Kongsfjorden clearly differed between the years (PERMANOVA, MS = 6079.7, Pseudo-F = 15.19, p = 0.001) and between the study periods only in 2015 (PERMANOVA post hoc, MS = 1782.3, Pseudo-F = 4.45, p = 0.013). *Calanus* copepodite stage structures were much more similar among study periods within one year than among corresponding study periods of the two years (Figure 6), which was indicated by higher estimated components of variance (ECV) for years other than for study periods (19.5% vs. 10.8%). The *Calanus* copepodite stage index in Kongsfjorden differed between years (PERMANOVA, MS = 698.1, Pseudo-F = 46.40, p = 0.001), but not between study periods (PERMANOVA, MS = 21.9, Pseudo-F = 1.46, p = 0.257). In general, in 2015 the median values of *Calanus* copepodite stage index were higher than in 2016, when they remained relatively low (Figure 7).
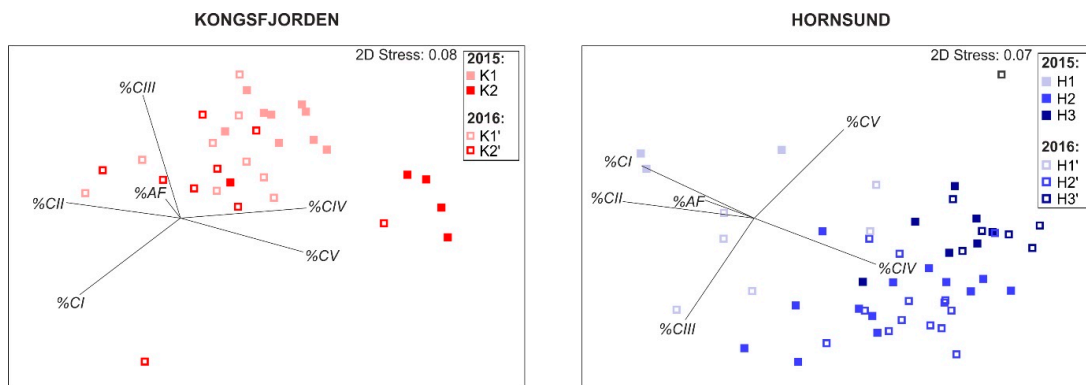
Figure 6. The non-metric multi-dimensional scaling (nMDS) of the *Calanus* copepodite structure in two Spitsbergen fjords: Kongsfjorden and Hornsund. Vectors indicate the direction of best correlating variables determined as a percentage of each copepodite stage. Their lengths correspond with the strength of the correlation.
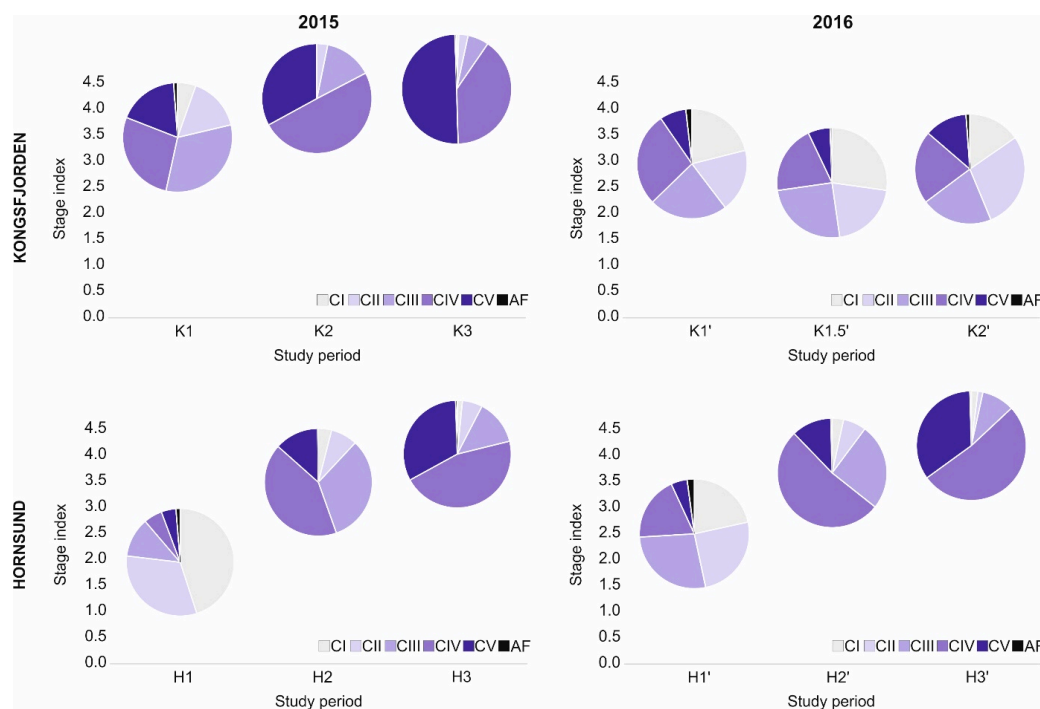

Figure 7. *Calanus* stage index (Y axis) together with copepodite stage structure (different colours) in Kongsfjorden and Hornsund in particular study periods (X axis) in 2015 and 2016.

The copepodite structure of *Calanus* in Hornsund differed first of all between study periods (PERMANOVA, MS = 3724.2, Pseudo-F = 31.16, p = 0.001), but also slightly between years (PERMANOVA, MS = 475.1, Pseudo-F = 3.98, p = 0.026; Figure 6). The higher share of ECV was obtained for the factor of periods than for a factor of year (15.9% vs. 4.4%). The *Calanus* copepodite stage index in Hornsund also differed between years (PERMANOVA, MS = 49.5, Pseudo-F = 7.62, p = 0.014) and study periods (PERMANOVA, MS = 746.9, Pseudo-F = 57.56, p = 0.001). Differences in the copepodite stage index had a stepwise character in both years, with a slightly higher median values in all investigated periods observed in 2016 (Figure 7).

Large differences in *Calanus* copepodite structure in Kongsfjorden were only observed in 2015, when the proportion of early copepodite stages (CI–CIII) decreased from over 50% in K1 to about 10% in K3 (Figure 7). The CIV was the dominating life stage in K2, then it was outnumbered by CV in K3. The proportion of AF was very low with a slightly higher value, but not exceeding 2% in K1. In 2016,

the composition of *Calanus* community was dominated by young copepodite stages and was very similar among study periods (Figure 7). The CI–CIII constituted approximately 60% of all copepodite stages with about 20% share for each stage. *Calanus* population in Hornsund in both years changed over time (Figure 7). Although the highest importance of the youngest copepodites of *Calanus* (CI and CII) were observed early in both years, (H1 and H1′), their contribution was almost two times higher in 2015 than in 2016. Thus, the correlation of these stages with the ordination coordinates was stronger concerning samples from 2015 (Figure 6). The highest proportion of CIII was observed in 2015 in H2 (31%) and in 2016 in both H1′ and H2′ (25%). The highest proportion of CIV was observed in the second and the third study periods in both years and was slightly higher in 2016. Peak occurrence of CV took place in the third period of both years (H3 and H3′). The proportion of AF was relatively low throughout the study, but slightly higher in the first study periods of both years and correlated positively with the youngest life stages.

The *Calanus* copepodite structure differed significantly between Hornsund and Kongsfjorden in corresponding periods only in 2016 (PERMANOVA, MS = 5558.3, Pseudo-F = 18.95, p = 0.001). In 2015, the copepodite structure in both fjords was relatively similar in corresponding periods H3 and K3 (PERMANOVA, MS = 642.8, Pseudo-F = 3.35, p = 0.054) with the predominance of late stages (CIV and CV) in both regions. In turn, in 2016 in the comparable H2′ and K1.5′ periods, the copepodite structure differed significantly, because of the high percentage of early stages CI–CIII recorded in Kongsfjorden, and the domination of CIV in Hornsund. Also the copepodite stage index for *Calanus* differed between two fjords only in 2016 (PERMANOVA, MS = 258.5, Pseudo-F = 34.61, p = 0.001), while in 2015 in corresponding study periods the stage index in H3 and K3 was similar (Figure 7). In analogous periods of 2016 (H2′ and K1.5′) a higher median value of stage index was observed in Hornsund (Figure 7).

4. Discussion

The phenology of *Calanus* is a critical factor for little auks reproduction success during their breeding season, as was shown recently in a spatial perspective study in Greenland [44] and in time perspective study in Svalbard waters [64]. Therefore it is now of vital importance to study the match in time and space between the availability of older life stages of *Calanus* and little auks, because as was shown by this study, the development rate and the age structure of *Calanus* may differ significantly depending on the region, water temperature and time in the season. The issue is alarming not only because temperature warming has been shown to accelerate development of *Calanus* [65], but also because the altered phenology of many species is becoming an increasingly important problem for trophic interactions [31,64,66] and thus entire food webs. To date, disturbance in interactions between predators and prey (match/mismatch) have been observed in many groups of organisms, e.g., between fish and plankton [67,68], insects and plants [69], birds and insects [70–72] shorebirds and arthropods [73] or seabirds and zooplankton [33,74,75]. The high variability in *Calanus* development, smaller body size and lower proportion in their concentration in relation to smaller zooplankton taxa in warmer Kongsfjorden, observed in our study, are in line with predicted scenarios of pelagic system modifications in the future Arctic towards faster development and prevailing role of smaller organism size [15,20,25]. Even though shortening life cycles and body size reduction of *Calanus* are expected not to have negative consequences for top predators [20], it will probably be important to the little auk, which is dependent on the availability of large, energy-rich prey [35].

Little auk preferentially search for large, lipid-rich copepods to cover the high energy costs incurred during foraging trips and feeding underwater [76–78]. Because the lipid content is strongly related to the body size, in this work *Calanus* size rather than species affiliation was utilized as the main qualitative trait. This approach is suggested as more appropriate for understanding the process of energy transfer to higher trophic levels on a larger scale [20]. Combining two species into one *Calanus* category was also supported by the recently discussed and clearly demonstrated problem of misidentification of *C. glacialis* and *C. finmarchicus* [17,19,20]. In order to gain a broader view on the *Calanus* population characteristics, in this study at the first step individuals of both species were

identified and separated in accordance with traditional morphological classification [55], by measuring the prosome length. Results have shown that neither the specimens classified as *C. glacialis* nor *C. finmarchicus* were following a normal size distribution (Figure 8), which was in opposition to what was demonstrated for this stage for both species by molecular methods [20] (Figure 1). A right-skewed size distribution of *C. glacialis* both in Hornsund and in Kongsfjorden observed in our study is most probably caused by the fact that larger individuals classified as *C. finmarchicus* are in fact smaller individuals of *C. glacialis* [20]. This confirms that the size criterion is no more a reliable tool to accurately classify an individual for a given species [79], thus justifying our approach to combine them into one group.
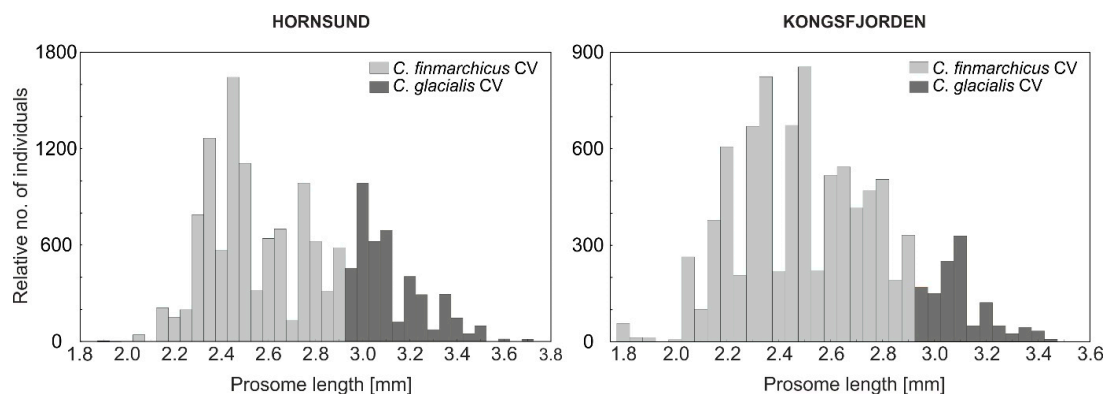

Figure 8. Prosome length frequency distribution of copepodite stage CV of *Calanus finmarchicus* and *C. glacialis* classified according to morphological identification after Kwasniewski et al. [55] in Hornsund (n = 1798) and Kongsfjorden (n = 799).

The body size of individual copepodite stages (CI–CV) of *Calanus* differed clearly between the two investigated fjords, with smaller prosome length observed in warmer Kongsfjorden than in colder Hornsund. First of all, such a difference may be explained by expected differences in proportions of *Calanus* species (*C. glacialis* vs. *C. finmarchicus*), which is also of importance for little auks [66]. But the change in individual size within particular species has also to be taken into consideration. Such observations are especially important in the light of recent studies demonstrating a great range of size plasticity of *Calanus* [17,19,20] and considering the fact that temperature is a key factor determining body size in copepods [21,80]. In this work, the smallest prosome length of *Calanus* CI-CV was observed at highest temperatures (>7 °C), whereas the largest individuals were observed in seawater temperature <4 °C. A similar trend was observed by LOPC measurements of *Calanus*-type particles selected for the older life stages, with the predominance of the largest individuals observed at temperatures below 4 °C and the smallest ones observed at temperatures above 6 °C in Hornsund. Such a clear differentiation in size modes can be explained by the co-occurrence of two water masses carrying two different *Calanus* species [14] and/or that the younger (CIV) copepodite stage was dominating in warmer, close to surface waters, while older (CV) life stage prevailed in colder conditions. Although the fraction of older *Calanus*-type particles was characterized by similar sizes in all temperature ranges in Kongsfjorden in 2015, the dominating size of this fraction was evidently shifted towards smaller sizes in the warmer season in 2016. This could be caused by different relative roles between CIV and CV life stages, or by the methodological bias, because the location of transects in both years slightly differed. In 2015 transects were performed closer to the interior part of the fjord, while in 2016 transects were mainly located in open shelf waters. Smaller individuals representing mainly *C. finmarchicus* can dominate in open waters with prevailing Atlantic water masses [19], while inside the fjord usually both species co-exist [17]. Hence the larger size of *Calanus*-type particles observed in 2015 could have resulted from a higher share of the larger species (*C. glacialis*). Despite differences in species composition, the significant relation between the body size of *Calanus* and seawater temperature observed in this study agrees with the assumptions of the temperature-size-rule (TSR) [81,82], which states that ectotherms grow

slower, but mature at a larger body size in colder environments. The smaller size of *Calanus* in warmer temperatures observed in this study may be explained by the fact that organisms tend to be smaller in response to warming [83–85] and progressive reduction of *Calanus* body size is predicted with increasing seawater temperatures [86]. The body size of *C. glacialis* was found to vary considerably along its geographical range [19,20,83,87]. In experimental studies on *C. finmarchicus*, its prosome length also significantly decreased with increasing sea temperatures. Moreover, the largest individuals of *C. glacialis* were recorded after development in waters with temperatures not exceeding 3 °C [16].

In addition to individual size of *Calanus*, the proportion of *Calanus* in the overall community is very important for visual planktivores such as little auks, which need their prey to occur not only in a high concentration but also as easily visible [37]. In general, *Calanus* species are the key element of zooplankton communities in Svalbard waters, especially in terms of biomass [1,88,89], however their proportion in total zooplankton abundance is highly variable in time, space and under different hydrographic conditions [63]. In this study the proportion of *Calanus* in total zooplankton abundance was higher in Hornsund than in Kongsfjorden in both studied years, which confirmed more favourable foraging conditions for little auks in Hornsund than Kongsfjorden [77,90]. A similar predominance of *Calanus* in Hornsund was also recorded in 2007 [91]. Likewise, Trudnowska et al. [92] found higher proportions of *Calanus* in zooplankton communities in the colder Hornsund than in the Atlantic-influenced Magdalenefjorden. The lower proportion of *Calanus* in Kongsfjorden could result from the strong advection of the Atlantic Water carrying high concentrations of small copepods (e.g., *Oithona similis*) [27,93,94]. Therefore, the Atlantic water masses are typically avoided by little auks, due to high proportions of small copepods, which hinder detection of preferred prey [14,37]. The abundance of *O. similis*, which was really high in Kongsfjorden in this study, has been increasing gradually in Spitsbergen fjords since 2006 [91] as a consequence of the progressive Atlantification of these waters [27]. The increasing importance of small copepods in the zooplankton composition [89] is one of the most spectacular examples of the progressing warming that have already been documented [23].

Studies of *Calanus* development are challenging because its reproductive strategies are highly variable in time and space due to corresponding changes in environmental conditions and food supply [6,20,86,95]. In this study the development of the *Calanus* population and in consequence also its stage index, followed similar trends in Hornsund in both years. A similar gradual development of *Calanus* population, reflected by a dominance of young stages CI–CIII during the first study period and older CIV–CV stages during the third period was observed in Rijpfjorden [6]. Such similarity in the *Calanus* age structure observed in Rijpfjorden and Hornsund indicates a coincident timing of reproductive events and its synchrony with ice algae bloom in April and phytoplankton bloom in July [96]. In addition, the presence of early copepodite stages in all the studied periods (this study) might suggest continuous reproduction, or at least, the presence of more than one generation of *Calanus*, which is likely in high latitudes according to several new studies [20,65,97]. In Kongsfjorden, the trend of a gradual population development was observed in this work only in 2015. This observation coincided with the seasonal dynamic of the *Calanus* population structure emphasized for this fjord by a year-round investigation of Lischka and Hagen [94] with a higher contribution of early copepodite stages in July and a more advanced population in August. In turn in 2016, *Calanus* age structure was very similar in all three studied periods in Kongsfjorden and persisted relatively young according to low stage index. To some extent this might be caused by shorter time intervals between sampling periods in this year, but most probably it was caused by different advection impacts, according to different sea surface temperatures in the two years investigated (Figure 9). The events of advection are often associated with a transport of younger populations [55,93,95], which could explain the higher contribution of early stages in 2016 in Kongsfjorden in K1' (7–8 °C SST, Figure 9). This fact was also confirmed by a multiyear study conducted in the WSC region, where the copepodite structure of *C. finmarchicus* was younger during 'warmer' than 'colder' summers [27].
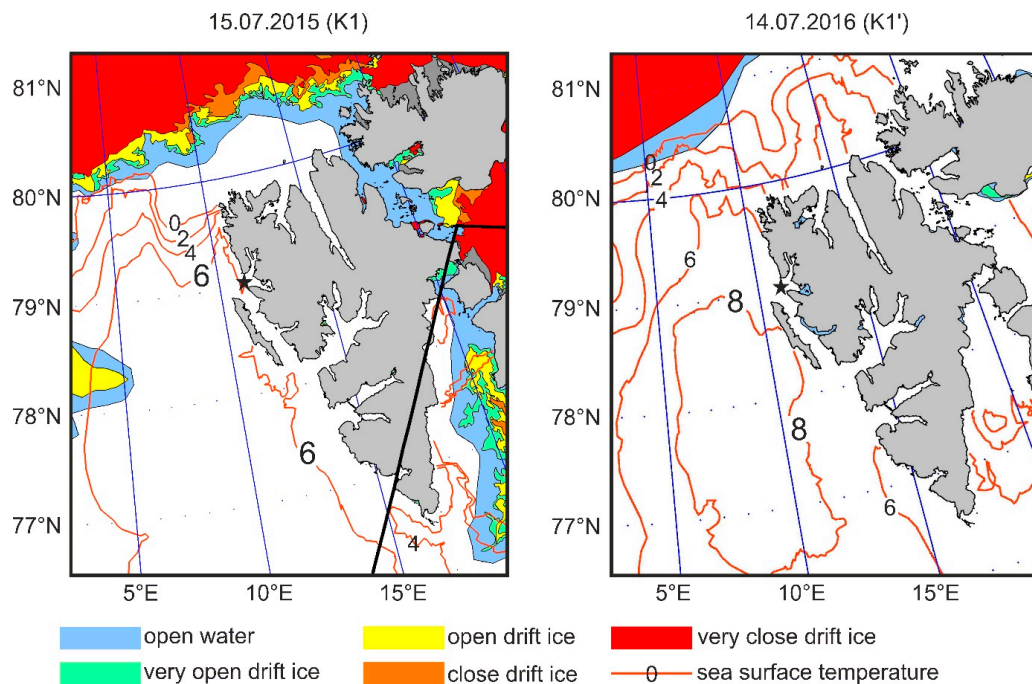
Figure 9. Sea surface temperature isoline and sea ice conditions (colour surfaces) in Svalbard waters in 2015 during K1 (**a**) and in 2016 during K1′ (**b**) study periods. Star icon represents Kongsfjorden study area. Data source: Norwegian Meteorological Institute.

5. Conclusions

This study confirms the difficulty in proper *Calanus finmarchicus* and *Calanus glacialis* recognition, which, together with the similar functions of these species proved in recent studies, was an important argument for aggregating them into a single *Calanus* group. This study also provides evidence that the development rate and size structure of *Calanus* is highly variable in time, space and in relation to seawater temperature. Furthermore, according to the observations of this research, the copepodite structure is much more dynamically affected by Atlantification in Kongsfjorden than in Hornsund. Additionally, seawater temperature was confirmed to correlate negatively with both the mean size of mesozooplankton organisms and the body length of *Calanus* copepodites (CI–CV). These results support the hypothesis about shortening the life span and associated reduction of the body size of *Calanus* along with climate warming. The accelerated development of *Calanus* can cause a significant shift in time in availability of its fifth copepodite stage in the foraging grounds of their key predator, the little auks. These findings confirm the hypothesis of the possible mismatch in timing between the availability of *Calanus* CV and the little auks highest food demands and therefore highlight the necessity to continue further seasonal studies of *Calanus* phenology in Svalbard waters.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Błachowiak-Samołyk, K.; Søreide, J.E.; Kwasniewski, S.; Sundfjord, A.; Hop, H.; Falk-Petersen, S.; Hegseth, E.N. Hydrodynamic control of mesozooplankton abundance and biomass in northern Svalbard waters (79–81°N). *Deep Sea Res. Part II Top. Stud. Oceanogr.* **2008**, *55*, 2310–2324. [CrossRef]

2. Carstensen, J.; Weydmann, A.; Olszewska, A.; Kwasniewski, S. Effects of environmental conditions on the biomass of *Calanus* spp. in the Nordic Seas. *J. Plankton Res.* **2012**, *34*, 951–966. [CrossRef]

3. Aarflot, J.M.; Skjodal, H.R.; Dalpadado, P.; Skern-Mauritzen, M. Contribution of *Calanus* species to the mesozooplankton biomass in the Barents Sea. *ICES J. Mar. Sci.* **2017**, *75*, 2342–2354. [CrossRef]

4. Scott, C.L.; Kwasniewski, S.; Falk-Petersen, S.; Sargent, J.R. Lipids and life strategies of *Calanus finmarchicus*, *Calanus glacialis* and *Calanus hyperboreus* in late autumn, Kongsfjorden, Svalbard. *Polar Biol.* **2000**, *23*, 510–516. [CrossRef]

5. Falk-Petersen, S.; Mayzaud, P.; Kattner, G.; Sargent, J. Lipids and life strategy of Arctic *Calanus*. *Mar. Biol. Res.* **2009**, *5*, 18–39. [CrossRef]

6. Daase, M.; Falk-Petersen, S.; Varpe, Ø.; Darnis, G.; Søreide, J.E.; Wold, A.; Leu, E.; Berge, J.; Philippe, B.; Fortier, L. Timing of reproductive events in the marine copepod *Calanus glacialis*: A pan-Arctic perspective. *Can. J. Fish. Aquat. Sci.* **2013**, *70*, 871–884. [CrossRef]

7. Melle, W.; Runge, J.; Head, E.; Plourde, S.; Castellani, C.; Licandro, P.; Pierson, J.; Jónasdóttir, S.; Johnson, C.; Broms, C.; et al. The North Atlantic Ocean as habitat for *Calanus finmarchicus*: Environmental factors and life history traits. *Prog. Oceanogr.* **2014**, *129*, 244–284. [CrossRef]

8. Kubiszyn, A.M.; Piwosz, K.; Wiktor, J.M., Jr.; Wiktor, J.M. The effect of inter-annual Atlantic water inflow variability on the planktonic protist community structure in the West Spitsbergen waters during the summer. *J. Plankton Res.* **2014**, *36*, 1190–1203. [CrossRef]

9. Ji, R.; Ashjian, C.J.; Campbell, R.G.; Chen, C.; Gao, G.; Davis, C.S.; Cowles, G.W.; Beardsley, R.C. Life history and biogeography of *Calanus* copepods in the Arctic Ocean: An individual-based modeling study. *Prog. Oceanogr.* **2012**, *96*, 40–56. [CrossRef]

10. Ackman, R.G. *Marine Biogenic Lipids, Fats and Oils*; CRC Press: Boca Raton, FL, USA, 1989.

11. Miller, C.B.; Crain, J.A.; Morgan, C.A. Oil storage variability in *Calanus finmarchicus*. *ICES J. Mar. Sci.* **2000**, *57*, 1786–1799. [CrossRef]

12. Lee, R.F.; Hagen, W.; Kattner, G. Lipid storage in marine zooplankton. *Mar. Ecol. Prog. Ser.* **2006**, *307*, 273–306. [CrossRef]

13. Mayzaud, P.; Falk-Petersen, S.; Noyon, M.; Wold, A.; Boutoute, M. Lipid composition of the three co-existing *Calanus* species in the Arctic: Impact of season, location and environment. *Polar Biol.* **2016**, *39*, 1819–1839. [CrossRef]

14. Kwasniewski, S.; Gluchowska, M.; Jakubas, D.; Wojczulanis-Jakubas, K.; Walkusz, W.; Karnovsky, N.; Blachowiak-Samolyk, K.; Cisek, M.; Stempniewicz, L. The impact of different hydrographic conditions and zooplankton communities on provisioning little auks along the west coast of Spitsbergen. *Prog. Oceanogr.* **2010**, *87*, 72–82. [CrossRef]

15. Wassmann, P.; Duarte, C.M.; Agustí, S.; Sejr, M.K. Footprints of climate change in the Arctic marine ecosystem. *Glob. Chang. Biol.* **2011**, *17*, 1235–1249. [CrossRef]

16. Parent, G.J.; Plourde, S.; Turgeon, J. Overlapping size ranges of *Calanus* spp. off the Canadian Arctic and Atlantic coasts: Impact on species' abundances. *J. Plankton Res.* **2011**, *33*, 1654–1665. [CrossRef]

17. Gabrielsen, T.M.; Merkel, B.; Søreide, J.E.; Johansson-Karlsson, E.; Bailey, A.; Vogedes, D.; Nygård, H.; Varpe, Ø.; Berge, J. Potential misidentifications of two climate indicator species of the marine arctic ecosystem: *Calanus glacialis* and *C. finmarchicus*. *Polar Biol.* **2012**, *35*, 1621–1628. [CrossRef]

18. Nielsen, T.G.; Kjellerup, S.; Smolina, I.; Hoarau, G.; Lindeque, P. Live discrimination of *Calanus glacialis* and *C. finmarchicus* females: Can we trust phenological differences? *Mar. Biol.* **2014**, *161*, 1299–1306. [CrossRef]

19.　Choquet, M.; Kosobokova, K.; Kwaśniewski, S.; Hatlebakk, M.; Dhanasiri, A.K.S.; Melle, W.; Daase, M.; Svensen, C.; Søreide, J.E.; Hoarau, G. Can morphology reliably distinguish between the copepods *Calanus finmarchicus* and *C. glacialis*, or is DNA the only way? *Limnol. Oceanogr. Methods* **2018**, *16*, 237–252. [CrossRef]

20.　Renaud, P.E.; Daase, M.; Banas, N.S.; Gabrielsen, T.M.; Søreide, J.E.; Varpe, Ø.; Cottier, F.; Falk-Petersen, S.; Halsband, C.; Vogedes, D.; et al. Pelagic food-webs in a changing Arctic: A trait-based perspective suggests a mode of resilience. *ICES J. Mar. Sci.* **2018**, *75*, 1871–1881. [CrossRef]

21.　Campbell, R.; Wagner, M.M.; Teegarden, G.J.; Boudreau, C.A.; Durbin, E.G. Growth and development rates of the copepod *Calanus finmarchicus* reared in the laboratory. *Mar. Ecol. Prog. Ser.* **2001**, *221*, 161–183. [CrossRef]

22.　Wilson, R.J.; Speirs, D.C.; Heath, M.R. On the surprising lack of differences between two congeneric calanoid copepod species, *Calanus finmarchicus* and *C. helgolandicus*. *Prog. Oceanogr.* **2015**, *134*, 413–431. [CrossRef]

23.　Richardson, A.J.; Schoeman, D.S. Climate impact on plankton ecosystems in the Northeast Atlantic. *Science* **2004**, *305*, 1609–1612. [CrossRef] [PubMed]

24.　Lane, P.V.Z.; Llinás, L.; Smith, S.L.; Pilz, D. Zooplankton distribution in the western Arctic during summer 2002: Hydrographic habitats and implications for food chain dynamics. *J. Mar. Res.* **2008**, *70*, 97–133. [CrossRef]

25.　Beaugrand, G.; Ibanez, F.; Lindley, J.A.; Reid, P.C. Diversity of calanoid copepods in the North Atlantic and adjacent seas: Species associations and biogeography. *Mar. Ecol. Prog. Ser.* **2002**, *232*, 179–195. [CrossRef]

26.　Woodworth-Jefcoats, P.A.; Polovina, J.J.; Drazen, J.C. Climate change is projected to reduce carrying capacity and redistribute species richness in North Pacific pelagic marine ecosystems. *Glob. Chang. Biol.* **2016**, *23*, 1000–1008. [CrossRef]

27.　Gluchowska, M.; Dalpadado, P.; Beszczynska-Möller, A.; Olszewska, A.; Ingvaldsen, R.B.; Kwasniewski, S. Interannual zooplankton variability in the main pathways of the Atlantic water flow into the Arctic Ocean (Fram Strait and Barents Sea branches). *ICES J. Mar. Sci.* **2017**, *74*, 1921–1936. [CrossRef]

28.　Haug, T.; Bogstad, B.; Chierici, M.; Gjøsæter, H.; Hallfredsson, E.H.; Høines, Å.S.; Hoel, A.H.; Ingvaldsen, R.B.; Jørgensen, L.L.; Knutsen, T.; et al. Future harvest of living resources in the Arctic Ocean north of the Nordic and Barents seas: A review of possibilities and constraints. *Fish. Res.* **2017**, *188*, 38–57. [CrossRef]

29.　Hjort, J. Fluctuations in the great fisheries of Northern Europe viewed in the light of biological research. *Reun. Cons. Int. Explor. Mer.* **1914**, *20*, 1–228.

30.　Cushing, D.H. Plankton production and year-class strength in fish populations: An update of the match/mismatch hypothesis. *Adv. Mar. Biol.* **1990**, *26*, 249–293.

31.　Stenseth, N.C.; Mysterud, A.; Ottersen, G.; Hurrell, J.W.; Chan, K.S.; Lima, M. Ecological effects of climate fluctuations. *Science* **2002**, *297*, 1292–1296. [CrossRef]

32.　Both, C.; Bouwhuis, S.; Lessells, C.M.; Visser, M.E. Climate change and population declines in a long-distance migratory bird. *Nature* **2006**, *441*, 81–83. [CrossRef] [PubMed]

33.　Hipfner, J.M. Matches and mismatches: Ocean climate, prey phenology and breeding success in a zooplanktivorous seabird. *Mar. Ecol. Prog. Ser.* **2008**, *368*, 295–304. [CrossRef]

34.　Nakazawa, T.; Doi, H. A perspective on match/mismatch of phenology in community contexts. *Oikos* **2012**, *121*, 489–495. [CrossRef]

35.　Kidawa, D.; Jakubas, D.; Wojczulanis-Jakubas, K.; Stempniewicz, L.; Trudnowska, E.; Boehnke, R.; Keslinka-Nawrot, L.; Błachowiak-Samołyk, K. Parental efforts of an Arctic seabird, the little auk *Alle alle*, under variable foraging conditions. *Mar. Biol. Res.* **2015**, *4*, 349–360. [CrossRef]

36.　Enstipp, R.; Descamps, S.; Fort, J.; Grémillet, D. Almost like a whale-first evidence of suction feeding in a seabird. *J. Exp. Biol.* **2018**, *221*, jeb182170. [CrossRef] [PubMed]

37.　Stempniewicz, L.; Darecki, M.; Trudnowska, E.; Błachowiak-Samołyk, K.; Boehnke, R.; Jakubas, D.; Keslinka-Nawrot, L.; Kidawa, D.; Sagan, S.; Wojczulanis-Jakubas, K. Visual prey availability and distribution of foraging little auks (*Alle alle*) in the shelf waters of West Spitsbergen. *Polar Biol.* **2013**, *36*, 949–955. [CrossRef]

38.　Mehlum, F.; Gabrielsen, G.W. The diet of high arctic seabirds in coastal and ice-covered, pelagic areas near the Svalbard archipelago. *Polar Res.* **1993**, *11*, 1–20. [CrossRef]

39.　Wojczulanis, K.; Jakubas, D.; Walkusz, W.; Wenneberg, L. Differences in food delivered to chicks by males and females of little auks (*Alle alle*) on South Spitsbergen. *J. Ornithol.* **2006**, *147*, 543–548. [CrossRef]

40.　Jakubas, D.; Wojczulanis-Jakubas, K. Subcolony variation in phenology in breeding parameters in little auk *Alle alle*. *Polar Biol.* **2011**, *34*, 31–39. [CrossRef]

41. Hovinen, J.E.H.; Wojczulanis-Jakubas, K.; Jakubas, D.; Hop, H.; Berge, J.; Kidawa, D.; Karnovsky, N.J.; Steen, H. Fledging success of little auks in the high Arctic: Do provisioning rates and the quality of foraging grounds matter? *Polar Biol.* **2014**, *37*, 665–674. [CrossRef]

42. Boehnke, R.; Gluchowska, M.; Wojczulanis-Jakubas, K.; Jakubas, D.; Karnovsky, N.J.; Walkusz, W.; Kwasniewski, S.; Błachowiak-Samołyk, K. Supplementary diet components of little auk chicks in two contrasting regions on the west Spitsbergen coast. *Polar Biol.* **2015**, *38*, 261–267. [CrossRef] [PubMed]

43. Boehnke, R.; Balazy, K.; Jakubas, D.; Wojczulanis-Jakubas, K.; Błachowiak-Samołyk, K. Meso-scale variations in little auk chicks diet composition in NW Spitsbergen. *Polar Res.* **2017**, *36*, 1409585. [CrossRef]

44. Møller, E.F.; Johansen, K.L.; Agersted, M.D.; Rigét, F.; Clausen, D.S.; Larsen, J.; Lyngs, P.; Middelbo, A.; Mosbech, A. Zooplankton phenology may explain the North Water polynya's importance as a breeding area for little auks. *Mar. Ecol. Prog. Ser.* **2018**, *605*, 207–223. [CrossRef]

45. Keslinka, L.K.; Wojczulanis-Jakubas, K.; Jakubas, D.; Neubauer, G. Determinants of the little auk (*Alle alle*) breeding colony location and size in W and NW coast of Spitsbergen. *PLoS ONE* **2019**, *14*, e0212668. [CrossRef] [PubMed]

46. González-Bergonzoni, I.; Johansen, K.L.; Mosbech, A.; Landkildehus, F.; Jeppesen, E.; Davidson, T.A. Small birds, big effects: The little auk (*Alle alle*) transforms high Arctic ecosystems. *Proc. R. Soc. B Biol. Sci.* **2017**, *284*, 20162572. [CrossRef]

47. Cottier, F.; Tverberg, V.; Inall, M.; Svendsen, H.; Nilsen, F.; Griffiths, C. Water mass modification in an Arctic fjord through cross-shelf exchange: The seasonal hydrography of Kongsfjorden, Svalbard. *J. Geophys. Res.* **2005**, *110*, C12005. [CrossRef]

48. Prominska, A.; Cisek, M.; Walczowski, W. Kongsfjorden and Hornsund hydrography-comparative study based on a multiyear survey in fjords of west Spitsbergen. *Oceanologia* **2017**, *59*, 397–412. [CrossRef]

49. Saloranta, E.; Svendsen, H. Across the Arctic Front west of Spitsbergen: High-resolution CTD sections from 1998–2000. *Polar Res.* **2001**, *20*, 174–184. [CrossRef]

50. Nilsen, F.; Cottier, F.; Skogseth, R.; Mattson, S. Fjord-shelf exchanges controlled by ice and brine production: The interannual variation of Atlantic Water in Isfjorden, Svalbard. *Cont. Shelf Res.* **2008**, *28*, 1838–1853. [CrossRef]

51. Sakshaug, E.; Johnsen, G.; Kovacs, K. *Ecosystem Barents Sea*; Tapir Academic Press: Trondheim, Norway, 2009.

52. Pavlov, A.K.; Tverberg, V.; Ivanov, B.V.; Nilsen, F.; Falk-Petersen, S.; Granskog, M.A. Warming of Atlantic Water in two Spitsbergen fjords over the last century (1912–2009). *Polar Res.* **2013**, *32*, 11206. [CrossRef]

53. Amélineau, F.; Bonnet, D.; Heitz, O.; Mortreux, V.; Harding, A.M.A.; Karnovsky, N.; Walkusz, W.; Fort, J.; Grémillet, D. Microplastic pollution in the Greenland Sea: Background levels and selective contamination of planktivorous diving seabirds. *Environ. Pollut.* **2016**, *219*, 1131–1139. [CrossRef] [PubMed]

54. Harris, R.; Wiebe, L.; Lenz, J.; Skjoldal, H.R.; Huntley, M. *ICES Zooplankton Methodology Manual*; Academic Press: London, UK, 2000.

55. Kwasniewski, S.; Hop, H.; Falk-Petersen, S.; Pedersen, G. Distribution of *Calanus* species in Kongsfjorden, a glacial fjord in Svalbard. *J. Plankton Res.* **2003**, *25*, 1–20. [CrossRef]

56. Herman, A.W. Design and calibration of a new optical plankton counter capable of sizing small zooplankton. *Deep-Sea Res. A* **1992**, *39*, 395–415. [CrossRef]

57. Herman, A.W.; Beanlands, B.; Phillips, E.F. The next generation of Optical Plankton Counter: The Laser-OPC. *J. Plankton Res.* **2004**, *26*, 1135–1145. [CrossRef]

58. Herman, A.W.; Harvey, M. Application of normalized biomass size spectra to laser optical plankton counter net intercomparisons of zooplankton distributions. *J. Geophys. Res.* **2006**, *111*, C5. [CrossRef]

59. Basedow, S.L.; Tande, K.S.; Norrbin, M.F.; Kristiansen, S.A. Capturing quantitative zooplankton information in the sea: Performance test of laser optical plankton counter and video plankton recorder in a *Calanus finmarchicus* dominated summer situation. *Prog. Oceanogr.* **2013**, *108*, 72–80. [CrossRef]

60. Anderson, M.J.; Gorley, R.N.; Clarke, K.R. *PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods*; Primer-E Ltd.: Plymouth, UK, 2008.

61. Clarke, K.R.; Gorley, R.N. *Primer*; Primer-E Ltd.: Plymouth, UK, 2001.

62. Anderson, M.J.; Braak, C.J.F. Permutation tests for multi-factorial analysis of variance. *J. Stat. Comput. Simul.* **2003**, *73*, 85–113. [CrossRef]

63. Kwasniewski, S.; Gluchowska, M.; Walkusz, W.; Karnovsky, N.J.; Jakubas, D.; Wojczulanis-Jakubas, K.; Harding, A.M.A.; Goszczko, I.; Cisek, M.; Beszczynska-Möller, A.; et al. Interannual changes in zooplankton on the West Spitsbergen Shelf in relation to hydrography and their consequences for the diet of planktivorous seabirds. *J. Mar. Sci.* **2012**, *69*, 890–901. [CrossRef]

64. Jakubas, D.; Wojczulanis-Jakubas, K.; Boehnke, R.; Kidawa, D.; Błachowiak-Samołyk, K.; Stempniewicz, L. Intra-seasonal variation in zooplankton avialability, chick diet and breeding performance of a high Arctic planktivorous seaird. *Polar Biol.* **2016**, *39*, 1547–1561. [CrossRef]

65. Weydmann, A.; Walczowski, W.; Carstensen, J.; Kwaśniewski, S. Warming of subarctic waters accelerates development of a key marine zooplankton *Calanus finmarchicus*. *Glob. Chang. Biol.* **2018**, *24*, 172–183. [CrossRef]

66. Jakubas, D.; Wojczulanis-Jakubas, K.; Iliszko, L.M.; Strøm, H.; Stempniewicz, L. Habitat foraging niche of a High Arctic zooplanktivorous seabird in a changing environment. *Sci. Rep.* **2017**, *7*, 16203. [CrossRef]

67. Ottersen, G.; Planque, B.; Belgrano, A.; Post, E.; Reid, P.C.; Stenseth, N.C.H. Ecological effects of the North Atlantic Oscillation. *Oecologia* **2001**, *128*, 1–14. [CrossRef] [PubMed]

68. Beaugrand, G.; Brander, K.M.; Lindley, J.A.; Souissi, S.; Reid, P.C. Plankton effect of cod recruitment in the North Sea. *Nature* **2003**, *426*, 661–664. [CrossRef] [PubMed]

69. Visser, M.; Holleman, L. Warmer springs disrupt the synchrony of oak and winter moth phenology. *Proc. R. Soc. B Biol. Sci.* **2001**, *268*, 289–294. [CrossRef] [PubMed]

70. Sanz, J.J.; Potti, J.; Moreno, J.; Merino, S.; Frias, O. Climate change and fitness components of a migratory bird breeding in the Mediterranean region. *Glob. Chang. Biol.* **2003**, *9*, 112. [CrossRef]

71. Thomas, D.W.; Blondel, J.; Perret, P.; Lambrechts, M.M.; Speakman, J.R. Energetic and fitness costs of mismatching resource supply and demand in seasonally breeding birds. *Science* **2001**, *291*, 2598–2600. [CrossRef]

72. Visser, E.M.; Adriaensen, F.; Van Balen, J.H.; Blondel, J.; Dhondt, A.A.; Van Dongen, S.; Du Feu, C.; Ivankina, E.V.; Kerimov, A.B.; De Laet, J.; et al. Variable responses to large-scale climate change in European Parus populations. *Proc. R. Soc. B Boil. Sci.* **2003**, *270*, 367–372.

73. McKinnon, L.; Picotin, M.; Bolduc, E.; Juillet, C.; Bêty, J. Timing of breeding, peak food availability, and effects of mismatch on chick growth in birds nesting in the High Arctic. *Can. J. Zool.* **2012**, *90*, 961–971. [CrossRef]

74. Mackas, D.L.; Batten, S.; Trudel, M. Effects on zooplankton of a warmer ocean: Recent evidence from the Northeast Pacific. *Prog. Oceanogr.* **2007**, *75*, 223–252. [CrossRef]

75. Bertram, D.F.; Mackas, D.L.; Welch, D.W.; Boyd, W.S.; Ryder, J.L.; Galbraith, M.; Hedd, A.; Morgan, K.; O'Hara, P.D. Variation in zooplankton prey distribution determines marine foraging distributions of breeding Cassin's Auklet. *Deep-Sea Res. Pap.* **2017**, *129*, 32–40. [CrossRef]

76. Konarzewski, M.; Taylor, J.R.E.; Gabrielsen, G.W. Chick energy requirements and adult energy expenditures of Dovekies (*Alle alle*). *Auk* **1993**, *110*, 603–609. [CrossRef]

77. Karnovsky, N.J.; Kwasniewski, S.; Weslawski, J.M.; Walkusz, W.; Beszczynska-Møller, A. The foraging behavior of little auks in a heterogeneous environment. *Mar. Ecol. Prog. Ser.* **2003**, *253*, 289–303. [CrossRef]

78. Jakubas, D.; Wojczulanis, K.; Walkusz, W. Response of dovekie to changes in food availability. *Waterbirds* **2007**, *30*, 421–428. [CrossRef]

79. Ragonese, S.; Bianchini, M.L. Growth, mortality and yield-per-recruit of the deep-water shrimp Aristeus antennatus (Crustacea-Aristeidae) of the Strait of Sicily (Mediterranean Sea). *Fish. Res.* **1996**, *26*, 125–137. [CrossRef]

80. Huntley, M.E.; Lopez, M.D.G. Temperature-dependent production of marine copepods: A global synthesis. *Am. Nat.* **1992**, *140*, 201–242. [CrossRef] [PubMed]

81. Atkinson, D. Temperature and organism size—A biological law for ectotherms? *Adv. Ecol. Res.* **1994**, *25*, 1–58. [CrossRef]

82. Angilletta, M.J.; Steury, T.D.; Sears, M.W. Temperature, growth rate, and body size in ectotherms: Fitting pieces of a life-history puzzle. *Integr. Comp. Biol.* **2004**, *44*, 498–509. [CrossRef]

83. Gillooly, J.F.; Brown, J.H.; West, G.B.; Savage, V.M.; Charnov, E.L. Effects of size and temperature on metabolic rate. *Science* **2001**, *293*, 2248–2251. [CrossRef]

84. Daufresne, M.; Lengfellner, K.; Sommer, U. Global warming benefits the small in aquatic ecosystems. *Proc. Natl. Acad. Sci. USA* **2009**, *106*, 12788–12793. [CrossRef]

85. Gardner, J.L.; Peters, A.; Kearney, M.R.; Joseph, L.; Heinsohn, R. Declining body size: A third universal response to warming? *Trends Ecol. Evol.* **2011**, *26*, 285–291. [CrossRef]

86. Banas, N.S.; Møller, E.F.; Nielsen, T.G.; Lisa, B.E. Copepod life strategy and population viability in response to prey timing and temperature: Testing a new model across latitude, time, and the size spectrum. *Front. Mar. Sci.* **2016**, *3*, 255. [CrossRef]

87. Leinaas, H.P.; Jalal, M.; Gabrielsen, T.M.; Hessen, D.O. Inter- and intraspecific variation in body- and genome size in calanoid copepods from temperate and arctic waters. *Ecol. Evol.* **2016**, *6*, 5585–5595. [CrossRef] [PubMed]

88. Daase, M.; Eiane, K. Mesozooplankton distribution in northern Svalbard waters in relation to hydrography. *Polar Biol.* **2007**, *30*, 969–981. [CrossRef]

89. Weydmann, A.; Carstensen, J.; Goszczko, I.; Dmoch, K.; Olszewska, A.; Kwasniewski, S. Shift towards the dominance of boreal species in the Arctic: Inter-annual and spatial zooplankton variability in the West Spitsbergen Current. *Mar. Ecol. Prog. Ser.* **2014**, *501*, 41–52. [CrossRef]

90. Brown, Z.W.; Welcker, J.; Harding, A.M.A.; Walkusz, W.; Karnovsky, N.J. Divergent diving behaviour during short and long trips of a bimodal forager, the little auk *Alle alle*. *J. Avian Biol.* **2012**, *43*, 215–226. [CrossRef]

91. Gluchowska, M.; Kwasniewski, S.; Prominska, A.; Olszewska, A.; Goszczko, I.; Falk-Petersen, S.; Hop, H.; Weslawski, J.M. Zooplankton in Svalbard fjords on the Atlantic-Arctic boundary. *Polar Biol.* **2016**, *39*, 1785–1802. [CrossRef]

92. Trudnowska, E.; Sagan, S.; Kwasniewski, S.; Darecki, M.; Blachowiak-Samaolyk, K. Fine-scale zooplankton vertical distribution in relation to hydrographic and optical characteristics of the surface waters on the Arctic shelf. *J. Plankton Res.* **2015**, *37*, 120–133. [CrossRef]

93. Willis, K.; Cottier, F.; Kwasniewski, S.; Wold, A.; Falk-Petersen, S. The influence of advection on zooplankton community composition in an Arctic fjord (Kongsfjorden, Svalbard). *J. Mar. Syst.* **2006**, *61*, 39–54. [CrossRef]

94. Lischka, S.; Hagen, W. Seasonal dynamics of mesozooplankton in the Arctic Kongsfjord (Svalbard) during year-round observations from August 1998 to July 1999. *Polar Biol.* **2016**, *39*, 1859–1878. [CrossRef]

95. Espinasse, M.; Halsband, C.; Varpe, Ø.; Gislason, A.; Gudmundsson, K.; Falk-Petersen, S.; Eiane, K. Interannual phenological variability in two North-East Atlantic populations of *Calanus finmarchicus*. *Mar. Biol. Res.* **2018**, *14*, 752–767. [CrossRef]

96. Søreide, J.E.; Leu, E.; Berge, J.; Graeve, M.; Falk-Petersen, S. Timing of blooms, algal food quality and *Calanus glacialis* reproduction and growth in a changing Arctic. *Glob. Chang. Biol.* **2010**, *16*, 3154–3163. [CrossRef]

97. Gluchowska, M.; Trudnowska, E.; Goszczko, I.; Kubiszyn, A.M.; Blachowiak-Samolyk, K.; Walczowski, W.; Kwasniewski, S. Variations in the structural and functional diversity of zooplankton over vertical and horizontal environmental gradients en route to the Arctic Ocean through the Fram Strait. *PLoS ONE* **2017**, *12*, e0171715. [CrossRef] [PubMed]