Chapter 7 Zooplankton in Kongsfjorden (1996–2016) in Relation to Climate Change



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Abstract Zooplankton in Kongsfjorden, Svalbard, is shaped by irregular advection of seawater from the West Spitsbergen Current as well as input of freshwater of glacial and riverine origin. The zooplankton community reflects contributions of Arctic vs. Atlantic water masses in the fjord, and is changing with increasing temperature and declining sea ice. Here, we review zooplankton studies from Kongsfjorden, and present new data from a 20-year time series (1996–2016) of zooplankton abundance/biomass in the fjord based on annual surveys during summer. During the last decade, the marine environment of the West Spitsbergen Shelf and adjacent fjords has undergone changes with increasing temperatures and volume of inflowing Atlantic Water and declining sea ice. Annual monitoring of meso-zooplankton since 1996 has shown high seasonal, spatial, and inter-annual variation

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© Springer Nature Switzerland AG 2019 H. Hop, C. Wiencke (eds.), *The Ecosystem of Kongsfjorden, Svalbard*, Advances in Polar Ecology 2, https://doi.org/10.1007/978-3-319-46425-1_7

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in species abundance and biomass, and in the proportion of Atlantic and Arctic species. Inter-annual variations in species composition and abundance demonstrate fluctuating patterns related to changes in hydrography. "Warm years" in Kongsfjorden were characterized by higher abundances of Atlantic species, such as Calanus finmarchicus, Oithona atlantica, Thysanoessa longicaudata and Themisto abyssorum. Other krill species, particularly Thysanoessa inermis and to a lesser extent T. longicaudata, increased in abundance during the warming period in 2006–2007, mainly in the inner basin. "Cold years", on the other hand, were characterized by higher abundance of Themisto libellula. There was no clear impact, however, of changes in environmental factors on the abundance or biomass of the Arctic species Calanus glacialis suggesting that the changes in environmental conditions have not reached critical levels for this species. The long-term zooplankton data demonstrate that some Atlantic species have become more abundant in the Kongsfjorden's pelagic realm, suggesting that they may benefit from increasing temperature, and also that the total biomass of zooplankton has increased in the fjord implying potentially higher secondary production.

Keywords Zooplankton \cdot Time-series \cdot Arctic water \cdot Sea ice \cdot Atlantification \cdot Advection \cdot Fjord \cdot Svalbard \cdot Arctic

7.1 Introduction

The Arctic Archipelago Svalbard is located in a border area between Atlantic and Arctic regimes. Kongsfjorden (78° 59 N, 11–12° E) is an open fjord on the west coast of Spitsbergen, the largest of Svalbard islands (Fig. 7.1a). Connection of the fjord to the adjacent shelf and Fram Strait is allowed through Kongsfjordrenna, a deep channel without sill. Kongsfjorden is therefore largely influenced by advection of both Arctic Water from the coastal current and Atlantic Water from the West Spitsbergen Current (WSC) (Svendsen et al. 2002). The inter-annual variation in the strength of the WSC influences the range of advection of water masses into the Arctic including Kongsfjorden (Saloranta and Svendsen 2001). During winter and spring, the advection between the fjord and the shelf may be limited due to a density front forming in the fjord entrance. This density front usually breaks down during

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Fig. 7.1 Sampling stations in (**a**) Fram Strait with deep Hausgarten Stations (HG, KH) and stations on the shelf and continental slope (V6, V10, V12) with Atlantic and Arctic currents, (**b**) Kongsfjorden, with main circulation patterns indicated outside and inside the fjord

spring and summer (Cottier et al. 2005) allowing warm Atlantic and transformed Atlantic water masses to enter the fjord at intermediate depths on the south side and circulate in the outer-middle part of the fjord (Fig. 7.1b). The density gradient has become less pronounced after 2006, leading to larger advection of Transformed Atlantic Water (TAW) into the fjord also during winter (Tverberg et al., Chap. 3). Some of the Atlantic-origin waters may continue above the shallow (20 m deep) sill into the inner basin of the fjord (Fig. 7.1b), which is largely influenced by glacial run off and calving of icebergs (Lydersen et al. 2014). The discharge of fresh water and sediments from glaciers peak during the summer melting (Sundfjord et al. 2017). Surface currents, which are influenced by winds and tides, generally flow out of the fjord due to katabatic winds coming down from the glaciers in the inner bay. These surface currents flow along the north side of the fjord and travel via Krossfjorden before exiting (Ingvaldsen et al. 2001).

Kongsfjorden is relatively easily accessible despite its high-Arctic location. A zooplankton monitoring program has been established there in 1996. During the last decade, remarkable changes have occurred in the ocean climate around Svalbard and in Kongsfjorden. The WSC has warmed since 2004, and the core of the Atlantic Water reached the highest temperatures in 2006 and 2011 (Walczowski et al. 2012; Gluchowska et al. 2017). Ocean warming and increased air temperatures have also influenced Kongsfjorden, particularly during the last 20 years, with a positive slope



Fig. 7.2 (a) Sea ice index (blue) at Northwest Spitsbergen and temperature in Kongsfjorden (red), and (b) Arctic Water (%) and Atlantic water (%) in Kongsfjorden, from 1996 to 2016. Grey shading indicates cold years, and dashed lines are the best fitting linear models

for the long-term trend (Fig. 7.2). Mooring records (2002–2017) have shown that the warming trend has been strongest during the coldest months of the year (Geoffroy et al. 2018; Hop et al., Chap. 13). During summer, the percentage of Arctic Water has decreased in the fjord, whereas Atlantic Water has increased (Fig. 7.2b). A comparison of oceanographic transects in Kongsfjorden for warm vs. cold years shows that the Atlantic Water (> 3.0 °C, S > 34.65) and Transformed Atlantic Water (1.0– 3.0 °C, S > 34.65) intrude further into the fjord during warm summers, and that the cold water masses are confined to the deep part of the fjord (Fig. 7.3).

Kongsfjorden used to have extensive fast-ice cover during winter, but a large inflow of Atlantic Water during the winter 2005–2006 (Cottier et al. 2007) forced the system into a warmer state with little fast-ice cover in the subsequent years, except for the winters of 2009 and 2011 when fast-ice was more extensive (Pavlova et al., Chap. 4). In the years after 2011, ice-coverage was limited to the inner part of the fjord for only short periods each year, and the ice has become progressively thinner with less snow on it during the monitored period 2003–2016 (Fig. 7.2a; Pavlova et al., Chap. 4).



Fig. 7.3 Salinity and temperature profiles from cold years (1996–2001, 2004–2005, and 2009–2011) combined and warm years (2002–2003, 2006–2008, and 2012–2016) combined

Due to the geographic and oceanographic setting, with influence from advection and local processes as well as sea-ice, the pelagic community of Kongsfjorden is composed of both Atlantic and Arctic species (Hop et al. 2006; Walkusz et al. 2009; Ormanczyk et al. 2017). The proportions of zooplankton species with different biogeographic origins vary with the dynamics of water masses outside the fjord and their changing intrusions (Kwasniewski et al. 2003; Basedow et al. 2004; Willis et al. 2006, 2008). Changes observed in zooplankton community composition from sediment traps at the central HAUSGARTEN site of Fram Strait are also reflected in Kongsfjorden, but variations may not be synchronous for the areas (Soltwedel et al. 2016). The circulation pattern within the fjord affects the advection of zooplankton and their residence time in the fjord (Kwasniewski et al. 2003; Basedow et al. 2004). Within the inner part of the fjord, zooplankton can potentially become exposed to glacial run off leading to increased mortality (Weslawski et al. 2000; Zajaczkowski and Legezynska 2001; Urbanski et al. 2017).

Kongsfjorden is one of the most studied fjords of the Svalbard archipelago and numerous studies have focused on different aspects of the zooplankton community, such as life history strategies and population dynamics of copepod species (Kwasniewski et al. 2003; Lischka and Hagen 2005, 2007; Willis et al. 2006, 2008; Narcy et al. 2009; Daase et al. 2013), krill (Buchholz et al. 2010, 2012; Dalpadado

et al. 2016), ctenophores (Falk-Petersen et al. 2002; Lundberg et al. 2006; Graeve et al. 2008), pteropods (Böer et al. 2005; Gannefors et al. 2005), seasonality (Walkusz et al. 2009; Lischka and Hagen 2016) and the effect of ocean climate variability on zooplankton communities (Hop et al. 2006). Recent studies (Dalpadado et al. 2016; Ormanczyk et al. 2017) indicate that the zooplankton community inside the fjord, containing a mix of resident and advected species, has changed substantially during the last decade. Other examples, such as studies from 1982 to 2016 on diet of black-legged kittiwakes (*Rissa tridactyla*) nesting in Kongsfjorden, have suggested changes in the pelagic food web towards "Atlantification" (Vihtakari et al. 2018).

This review consists of two parts. In Part I: Zooplankton community composition in Kongsfjorden, we review studies of different aspects of zooplankton ecology in Kongsfjorden, with emphasis on recent literature since Hop et al. (2006). In Part II: Trends in the zooplankton time-series, we: (1) Present unpublished time-series data obtained during the last 20 years (1996–2016) covering hydrography as well as zooplankton abundance and biomass. This dataset represents the longest record of its kind for an Arctic fjord. (2) Increase insight on possible climate and ocean change processes. In particular, we assess whether inter-annual differences in zooplankton abundance and biomass can be related to "cold-" and "warm-year" conditions in the fjord and whether observed long-term changes may be attributed to an increased "Atlantification" after a warming event in 2006 (Fig. 7.2; Cottier et al. 2007).

7.2 Materials and Methods

7.2.1 Sampling During 20-Year Time Series

Zooplankton has been sampled annually at standard stations in Kongsfjorden between 1996 and 2016 during July–August (dates include 13 July–28 August), except for 1998 (when no summer samples were taken). Sampling has been conducted along a transect including three stations in the inner basin (Kb7, Kb6, Kb5), five stations in the outer basin (Kb4, Kb3, Kb2, Kb1, Kb0), two stations at the shelf (V12, V10), and four stations off the shelf (V6, KH, HG-I, HG-IV; Table 7.1 and Fig. 7.1b). Depth-specific measurements of temperature and conductivity have been conducted prior to net sampling at each station using a ship-boarded CTD (Sea-Bird Electronics SBE911 plus). The vertical distribution of mesozooplankton was determined using a multiple plankton sampler (MultiNet type Midi, Hydro-Bios Kiel), consisting of five closing nets with 200 µm mesh size and 0.25 m² mouth opening.

Samples for taxonomical analyses were preserved in 4% hexamethylenetetraminebuffered seawater formaldehyde solution immediately after collection. The organisms were identified and counted under a stereomicroscope equipped with an ocular micrometre, according to standard procedures (Postel et al. 2000; Kwasniewski et al.

	2016	1	I	I		1	I	I	I	I	I	I			
	2015	I	I	I		I	I	I	I	I	I				
	2014	I	I	I		I	I	I	I	I	I	I		I	ı
	2013	I	I	I		I	I	I	I	I	I	I	I		ı
	2012			I		I	I	I	I	I	I	I	I		ı
	2011			I		I	I	I	I	I	I				
	2010			I		I	I	I	I	I	I	I			
	2009			I	I	I	ı	I	I	I	I	I			
	2008			ı		I	ı	I	I	I	I				
	2007					I	ı	I	I		I	I			
	2006			I		I	I	I	I	I	I	I			
	2005			I		I	I	I	I						
	2004			I		I	ı	I	I	I	I	I			
	2003			I		I	I	I	I						
	2002			I		I	I	I	I		I	I			
	2001			I		I	I	I	I			I			
)	2000			ı		1	1	ı	ı						
i N	1999					I	ı	I							
	1998														
	1997					1		1							
	1996					1	1	1							
- (B. depth [m]	62	71	96	93	329	330	352	315	224	291	1125	1150	1246	1850
	Longitude [E]	12° 22.79	12° 23.11	12° 26.45	12° 11.79	11° 57.38	11° 43.91	11° 25.66	11° 08.36	09° 29.77	08° 32.82	07° 46.24	07° 00.00	06° 05.54	04° 36.00
	Latitude [N]	78° 57.99	78° 55.80	78° 53.79	78° 54.63	78° 57.24	78° 58.68	79° 00.67	79° 02.78	78° 58.79	78° 55.96	78° 54.39	79° 03.00	79° 08.00	79° 06.48
	Station	Kb7	Kb6	Kb5	Kb4	Kb3	Kb2	Kb1	Kb0	V12	V10	V6	КН	HG-I	HG-IV
	Area	Inner basin				Outer basin				Shelf		Shelf break	Fram Strait		

 Table 7.1
 Stations sampled (-) in Kongsfjorden, Svalbard 1996–2016

2003). In the laboratory, each zooplankton sample was first scanned for macro-zooplankton (organisms with total length > 5 mm), which were picked out, identified and counted in the entirety. The remaining mesozooplankton size fraction was examined for taxonomic composition and abundance by a subsampling method (Postel et al. 2000). Subsamples of 2-ml volume were taken using a macropipette (an equivalent of the Stempel pipette) and all organisms in each subsample were identified and enumerated. Subsampling was continued until at least 500 individuals per sample were identified (Postel et al. 2000). *Calanus* spp. were identified to species for each developmental stage based on the description by Kwasniewski et al. (2003). Other zooplankters were identified to the lowest possible taxonomic level based on available literature.

Zooplankton species found in Kongsfjorden were grouped into main taxonomic groups or size-groups for copepods. *Calanus finmarchicus* and *C. glacialis* were kept as separate species due to their significant contribution to the mesozooplankton biomass. Small copepods were defined as copepods <2.5 mm total length as adults, which mainly included *Oithona similis, Pseudocalanus* spp. and *Microcalanus* spp. Other copepods encompassed copepod species >2.5 mm, excluding *Calanus* spp. Meroplankton comprised Cirripedia nauplii and cypris, and larval stages of Bivalvia, Bryozoa, Echinodermata, Gastropoda and Polychaeta. Other crustaceans included amphipods, euphausiids, cumaceans, mysids, decapods, isopods, ostracods, cladocerans and tanaidaceans. Other zooplankton were non-crustacean zooplankters such as hydrozoans, ctenophores, appendicularians, chaetognaths, pteropods, polychaetes, nemerteans, and larval fishes.

Original data represent abundance values of zooplankters (ind. m^{-3}) for different depth strata (bottom-200-100-50-20-0 m or bottom-600-200-50-20-0 m). Abundance values were converted to biomass estimates (mg dry mass m^{-3}) for statistical comparisons, to reduce potential bias caused by small copepodid stages, which can outnumber older stages seasonally, and for which occurrence can vary from year to year. The dry mass conversion factors were gathered from published sources or measured by the authors (Appendix Table 7.8). The biomasses/abundances for each species or a group of species were summed up by stage, size group and/or species and averaged over depth strata for each station:

$$\sum_{i=1}^{n} \frac{a_i d_i}{d_i}$$

Where a_i is the biomass or abundance of species a at depth stratum i, d_i is the sampled distance for depth stratum i in meters, and n is the number of depth strata per net haul at a station. Resulting averaged estimates for species or a group of species for separate net hauls at each station were used as statistical replicates by grouping the stations according to the Inner basin, the Outer basin, the Shelf, and Fram Strait, named as regions from here on.

7.2.2 Macrozooplankton Sampling

The MultiNet used in our time series has been used during many other studies performed in Kongsfjorden making our observation comparable (Appendix Table 7.9). Amphipods and euphausiids were regularly present in our MultiNet time-series (see Fig. 7.7), but are generally undersampled by this type of net (Pearcy et al. 1983; Søreide et al. 2003; Blachowiak-Samolyk et al. 2017). We therefore combined the abundance and biomass estimates of amphipods and euphausiids from the Multinet with data retrieved from MIK and Tucker Trawl hauls in Kongsfjorden, when considering seasonal variability (Fig. 7.8). The MIK net (2-m diameter opening, 14 m long with main net bag of 1.2 mm mesh size, and the terminal 1.5-m part of 0.5 mm mesh size) has been deployed at the same stations and times as the MultiNet since 2006. Vertical hauls with MIK were taken from ~20 m above the bottom to the surface at a speed of 0.5 ms⁻¹ (see Dalpadado et al. [2016] for details). For population dynamics of krill, we included data collected in Kongsfjorden since 2006 with an opening/closing Tucker Trawl with 1 mm mesh size, towed obliquely from near bottom (95–200 m) to the surface (see Buchholz et al. [2010] for details).

7.2.3 Statistical Analyses

Spatial and temporal differences were examined using mean values, bootstrapped confidence intervals (Davison and Hinkley 1997; Canty and Ripley 2017), and nonparametric statistical tests (Kruskal-Wallis [R Core Team 2018], and Dunn's Kruskal-Wallis multiple comparisons (Dunn 1964; Ogle 2018). The difference in biomass between cold and warm years was visualized using logarithmic response ratios (LnR) and 95% confidence intervals for LnR estimates using a t-distribution instead of normal distribution as described in Hedges et al. (1999). The significance (alpha level 0.05) of LnR estimates was confirmed using nonparametric two-sample Wilcoxon tests (R Core Team 2018). Patterns in zooplankton community structure were related to explanatory variables (sampling depth, average temperature and salinity, year, location of station along the transect, region, type of year [warm vs. cold]) using a principal component analysis (PCA) and redundancy analyses (RDA; Oksanen et al. 2018) on natural logarithm +1 transformed zooplankton abundance estimates. For this type of analysis, abundance gives a more detailed pattern than biomass, which is dominated by a few bulky species. The best fitting explanatory variables, assessed using the envfit function from Oksanen et al. (2018), were further used to constrain the ordinations, which were split to Inner and Outer basin stations and to Shelf and Fram Strait stations to avoid interactions that were present in the dataset.

7.2.4 Contribution of Arctic and Atlantic Water Masses in the Fjord

Percentage contribution of Arctic and Atlantic Water at each station in the Inner and Outer basin was estimated from CTD data accompanying each depth-stratified MultiNet catch, as statistical replicates. The water type definition followed Cottier et al. (2005) and was determined from averaged temperature and salinity values from CTD casts for each depth stratum sampled by MultiNet. Consequently, a single water type was allocated to each depth stratum representing average conditions for the MultiNet sample. Percentage contribution of Arctic and Atlantic water-type zooplankton species was calculated for each sampling event by dividing the corresponding zooplankton counts by the total number of depth strata (typically 5 or 6). These percentages were then used to calculate average water-type contributions in the fjord, with bootstrapped 95% confidence intervals for each year. The water-type definition algorithm is included in the PlotSvalbard package (define_water_type; Vihtakari 2018). All statistics were run using R (R Core Team 2018).

7.3 Part I: Zooplankton Community Composition in Kongsfjorden

7.3.1 Zooplankton Taxa in Kongsfjorden

In total 92 species and five genera have been identified in zooplankton samples from Kongsfjorden, and some organisms were identified to higher taxonomic levels, particularly for phyla including meroplankton (Table 7.2). Most of these species were included in our long-term series (1996-2016), as specific groups or lumped as others (Figs. 7.4 and 7.5). Our data show that the mesozooplankton community in Kongsfjorden was dominated by copepods (43 species or 47 taxa, with some identifications to higher level than species; Fig. 7.4). In terms of numbers, small-sized (< 2.5 mm) copepods such as Oithona similis, Pseudocalanus spp. and Microcalanus spp. generally dominated. Calanus finmarchicus and C. glacialis were the most common larger calanoid copepods. Other important groups were amphipods (10 species), typically consisting of the pelagic hyperiid Themisto abyssorum and Themisto libellula and other, less frequently found mesopelagic (e.g. Scina borealis) or ice-associated species (Apherusa glacialis and Gammarus wilkitzkii), euphausiids (4 species, mainly Thysanoessa raschii, T. inermis, and T. longicaudata) and Other Crustacea. Meroplankton (12 taxa) was among the abundant groups and included mainly larval forms of bivalves, echinoderms, polychaetes, and cirripedes, as well as decapod zoea larvae of shrimps (Pandalus borealis and Sabinea septemcarinata). Cnidarians (10 taxa) included different species of Hydrozoa with numerical dominance of Aglantha digitale, and not identified

Table 7.2 List of species and taxa found in zooplankton samples from Kongsfjorden in different studies (see Appendix Table 7.8). Taxa collected in the annual surveys (1996–2016) are indicated (*), and these are summarized in Fig. 7.4. Some species are present in the plankton as larval forms (L)

Copepoda (Arthrop	oda)		
Calanoida			
Acartia longiremis*	Microcalanus spp.*	Spinocalanus horridus*	Harpacticoida
Aetideopsis minor*	Neoscolecithrix farrani*	Spinocalanus longicornis*	Harpacticoida indet.*
Aetideopsis rostrata*	Paraeuchaeta barbata*	Temora longicornis	Microsetella norvegica*
Aetideus armatus*	Paraeuchaeta glacialis*	Temorites brevis*	Monstrilloida
Augaptilus glacialis*	Paraeuchaeta norvegica*	Tharybis groenlandicus*	Monstrilloida indet.*
Bradyidius similis*	Paraheterorhabdus compactus*	Undinella oblonga*	Mormonilloida
Calanus finmarchicus*	Pertsovius fjordicus	Xantharus siedleckii*	Neomormonilla minor*
Calanus glacialis*	Pleuromamma robusta*	Cyclopoida	Siphonostomatoida
Calanus hyperboreus*	Pseudocalanus acuspes*	Cyclopoida indet.*	Hyalopontius sp.
Chiridius obtusifrons*	Pseudocalanus minutus*	Homeognathia brevis*	
Gaetanus brevispinus*	Pseudochirella spectabilis*	Oithona atlantica*	
Gaetanus tenuispinus*	Rhincalanus nasutus*	Oithona similis*	
Heterorhabdus norvegicus*	Scaphocalanus brevicornis*	Oncaea parila*	
Mesaiokeras spitsbergensis*	Scaphocalanus magnus*	Oncaea pumilis	
Metridia longa*	Scolecithricella minor*	Triconia borealis*	
Metridia lucens*	Spinocalanus antarcticus*	Triconia conifera*	
Other Crustacea (A	rthropoda)		
Amphipoda	Euphausiacea	Decapoda	Ostracoda*
Apherusa glacialis*	Meganyctiphanes norvegica*	Eusergestes arcticus*	Boroecia borealis
Cyclocaris guilelmi*	Nematoscelis megalops	Hyas araneus (L)*	Boroecia maxima
Eusirus holmii*	Thysanoessa inermis*	Hymenodora glacialis*	Discoconchoecia elegans
Hyperia galba*	Thysanoessa longicaudata*	Pagurus pubescens (L)*	Obtusoecia obtusata
Hyperoche medusarum*	Thysanoessa raschii*	Pandalus borealis (L)*	Cladocera
Onisimus glacialis*	Cumacea	Sabinea septemcarinata (L)*	Evadne nordmanni*

(continued)

Scina borealis*	Leucon sp.*	Isopoda	Tanaidacea
Themisto abyssorum*	Mysida	Bopyridae indet. (L)*	Cirripedia*
Themisto libellula*	Boreomysis arctica*	Isopoda indet. (L)*	
Gammarus wilkitzkii*	Pseudomma truncatum*		
Other phyla			1
Cnidaria	Anthozoa (L)	Annelida	Echinodermata (L)*
Hydrozoa	Ctenophora	Polychaeta (L)*	Chaetognatha
Aeginopsis laurentii*	Mertensia ovum*	Pelagobia sp.*	Eukrohnia hamata*
Aglantha digitale*	Beroë cucumis*	Tomopteris spp.*	Parasagitta elegans*
Botrynema ellinorae*	Mollusca	Typhloscolecidae (L)*	Pseudosagitta maxima*
Bougainvillia spp.*	Bivalvia (L)*	Nematoda	Chordata
Dimophyes arctica*	Pteropoda	Nemertea (L)*	Appendicularia
Halitholus cirratus*	Clione limacina*	Platyhelminthes	Fritillaria borealis*
Nanomia cara*	Limacina helicina*	Turbellaria	Oikopleura vanhoeffeni*
Sarsia spp.*	Limacina retroversa*	Bryozoa (L)*	Oikopleura labradoriensis*
Siphonophora*	Gastropoda (L)*	Rotifera	Ascidiacea (L)*
Scyphozoa*	Cephalopoda*	Enteropneusta (L)	Pisces (L)*

Table 7.2 (continued)

species of Siphonophora and Scyphozoa. The ctenophores *Beroë cucumis* and *Mertensia ovum* were typically present, as were pteropods (*Limacina helicina*, *L. retroversa* and *Clione limacina*) and chaetognaths (*Parasagitta elegans*, *Eukrohnia hamata* and *Pseudosagitta maxima*). Chordates were larval fishes and appendicularians (*Fritillaria borealis*, *Oikopleura venhoffeni* and *O. labradorensis*).

Species of Arctic origin included the copepods *C. glacialis, Triconia borealis, C. hyperboreus* and *Pseudocalanus acuspes*, the amphipod *T. libellula*, and the cnidarian *Aglantha digitale*. Species representative of Atlantic water masses typically included the copepods *C. finmarchicus* and *Oithona atlantica*, the amphipod *T. abyssorum*, the pteropod *L. retroversa*, and the euphausiids *T. longicaudata* and *Meganyctiphanes norvegica*.

7.3.2 Small- to Medium-Sized Copepods

Small-to medium-sized copepods (<2.5 mm in length at their adult stage) are mainly represented by the genera *Microcalanus*, *Pseudocalanus*, *Oithona* and *Triconia*. These are species that generally occur in high numbers during most of the year, have herbivorous or omnivorous feeding patterns, high weight-specific ingestion rates

and may produce offspring throughout the year (Svensen et al. 2011). They generally contribute little to biomass because of their small body sizes, but can be important grazers on the small phytoplankton fraction (<10 μ m). However, these species - and in particular their young copepodid stages - are typically undersampled in zooplankton surveys, unless finer mesh sizes (60–90 μ m) are used for collecting samples.

Among small copepods, the cyclopoid O. similis is the most dominant species in Kongsfjorden throughout the year contributing with 30-80% to the abundance of holoplankton and peaking in abundance towards the winter season (November) (Hop et al. 2002; Lischka and Hagen 2005; Piwosz et al. 2009; Walkusz et al. 2009; Kwasniewski et al. 2013; Gluchowska et al. 2016; Ormanczyk et al. 2017). Although small in size, the standing stock biomass of O. similis in Kongsfjorden can amount to 0.6-17% of the zooplankton biomass of the size fraction from 0.2 to 10 mm during summer-early autumn (Hop et al. 2002; Ormanczyk et al. 2017); our long-term dataset indicates 2% on average within 0.1-9.0% range. Oithona similis is a cosmopolitan species adapted to a wide range of environmental conditions (Fransz and Gonzalez 1995; Gallienne and Robins 2001; Ward and Hirst 2007). Because of this ability, O. similis may benefit from the on-going temperature increase in the Arctic (Narcy et al. 2009) possibly due to shorter life span with increasing temperature (Huntley and Lopez 1992; Møller et al. 2012). A large increase in abundance of O. similis in Kongsfjorden during the earlier warming period (2001-2003) in Kongsfjorden supports this notion (Hop et al. 2006; Willis et al. 2006).

Oithona similis is an opportunistic omnivorous feeder that also uses detritus, faecal pellets and particle-associated bacteria as food source (Kattner et al. 2003; Castellani et al. 2005; Lischka and Hagen 2007). This allows the species to reproduce continuously throughout the year with two main reproductive periods in May/ June and August/September. Accordingly, all copepodid stages occur throughout the year in Kongsfjorden, although in varying proportions (Lischka and Hagen 2005). The species stays active in the upper water column also during winter (Conover and Huntley 1991; Lischka et al. 2007).

The role of lipid storages in *O. similis* has been thoroughly studied in Kongsfjorden. *Oithona similis* stores lipids in form of wax esters and to some extent also triacylgylcerols (Narcy et al. 2009). Winter survival, development, gonad maturation, egg production and the first main reproductive period in May/June are at least partially fuelled by internal lipid reserves that are continuously depleted during the dark season while replenishment of storage lipids occurs in late summer (August/September), along with still on-going reproductive processes (Lischka and Hagen 2007; Lischka et al. 2007). According to Narcy et al. (2009), the realization of *O. similis*' life cycle strategy may vary inter-annually and the lipid stores might be more of an adaptation to short-term food variability than to seasonal variation. In contrast to Lischka and Hagen (2005), Narcy et al. (2009) showed an increase in wax ester content in *O. similis* females and CV copepodids even before the maximum accumulation of phytoplankton biomass in spring and subsequent usage of these lipids during the main reproductive period in June. This indicates that *O. similis* can utilize other food sources, including particulate organic matter of high



Fig. 7.4 Numbers of taxa (species and higher taxonomic groups) in the mesozooplankton samples collected in Kongsfjorden during 1997–2016 by MultiNet (200 μ m mesh size). Numbers marked with question mark include higher level unidentified taxa and actual species numbers are uncertain

nutritional value (i.e. with high proportion of polyunsaturated fatty acids), to accumulate storage lipids in spring.

Oithona atlantica occurs regularly in Kongsfjorden, but is much less abundant than its congener *O. similis*. Throughout the year, the share of *O. atlantica* to the mesozooplankton abundance is generally <1% (e.g. Hop et al. 2006; Piwosz et al. 2009; Walkusz et al. 2009; Lischka and Hagen 2016). In our time series, we detected a trend of increasing abundance of *O. atlantica* between the years 2000 and 2002 (Hop et al. 2006), while the mean contribution of the species to the mesozooplankton community abundance was approximately 1% (range 0–5.2%).

Two *Microcalanus* species, *M. pygmaeus* and *M. pusillus*, and one *Triconia* species, *T. borealis* occur in Kongsfjorden (Walkusz et al. 2009). Compared to *O. similis* and *Pseudocalanus* sp. (see below) they constitute a much lower share of the total mesozooplankton abundance. *Microcalanus* spp. and *T. borealis* are relatively abundant year-round with clear peak in abundance in November (Lischka and Hagen 2016). Their seasonal contributions to mesozooplankton abundance range from 0–9% to 0–6%, respectively (e.g. Walkusz et al. 2003, 2009; Hop et al. 2002, 2006; Kwasniewski et al. 2013; Gluchowska et al. 2016; Ormanczyk et al. 2017). Our long-term data indicate that *Microcalanus* spp. was on average more abundant (3.0%) than *T. borealis* (1.5%). However, Lischka and Hagen (2016) found that abundance proportions of these species varied seasonally, for *Microcalanus* spp. from 0.1% (September 1998) to 29% (May 1999), and for *T. borealis* from 2% (May 1999) to 12% (August 1998). The distinctly higher proportions in their study were likely related to the use of a finer mesh size of 100 µm. In studies using 180–200 µm



Fig. 7.5 Spatial distribution of zooplankton biomass along the Kongsfjorden transect from Fram Stait to the Inner fjord basin, combined for the years 1996–2016 based on MultiNet (200 μ m mesh size) samples. Height of bars indicate the average zooplankton biomass using biomass values from stations sampled during different years as statistical replicates. Stacked coloured parts indicate the contribution of each zooplankton group to this total biomass. Error bars indicate bootstrapped 95% confidence intervals for the total mean biomass estimate. Cnidaria and Ctenophora have been excluded from the estimates due to non-representative sampling of these phyla

mesh size, *Microcalanus* spp. and *T. borealis* typically make up about 1% of the biomass in the small and medium zooplankton size-fraction (Ormanczyk et al. 2017), or less (0.45%) as observed in our long-term data. These species predominantly dwell below 50 m depth in Kongsfjorden (Walkusz et al. 2009; Lischka and Hagen 2016). *Microcalanus* spp. has two major reproductive periods, in February/ March and in June/July. For *T. borealis*, year-round reproductive activities have been suggested with a peak in May/June (Lischka and Hagen 2016).

Pseudocalanus is among the most dominant herbivorous copepod genera and the second-most abundant small copepod in Kongsfjorden, but it is clearly less abundant than *O. similis* (Table 7.3; Piwosz et al. 2009; Walkusz et al. 2009; Gluchowska et al. 2016; Ormanczyk et al. 2017). As for *O. similis*, *Pseudocalanus* spp. has increased in abundance in Kongsfjorden since 1996 (Hop et al. 2006). Lischka and Hagen (2016) observed high variability in the percent contribution of *Pseudocalanus* spp. to the mesozooplankton community from 1% (June 1999) to 31% (September 1998). Walkusz et al. (2009) similarly reported 0.8% in spring (April) and 21% in autumn (September). Abundance peaks of *Pseudocalanus* spp. have been observed late in autumn (November) prior to their overwintering (Lischka and Hagen 2005), and the relative abundance of the species may occasionally be high in late winter-early spring (e.g. 28% in March 1999; Lischka and Hagen 2016). The abundance of

Table 7.3 Abundance (ind. m^{-3}) of copepods in Kongsfjorden during the periods 1996–2006 and 2007–2016, averaged over all sampled stations. The copepodid developmental stages (from stage 1 to stage 6 female or male, C1–C6F/M, which contributed to the summary presented, are listed next to the species names. No specified stage indicates all copepodids C1–C6 are included

	1996-2006		2007-2016	
	All stations		All stations	
Copepoda	Mean ± StDev	Max	Mean ± StDev	Max
Acartia longiremis	4.8 ± 10.9	49.9	4.2 ± 6.9	29.0
Aetideidae indet. C1–C3	0.6 ± 1.7	7.6	1.6 ± 2.4	15.9
Aetideopsis minor C4–C6	0.0 ± 0.0	0.1	0.1 ± 0.6	5.9
Aetideopsis rostrata C4–C6	0.0 ± 0.0	0.0	0.0 ± 0.1	0.4
Aetideus armatus C4–C6	0.0 ± 0.0	0.0	0.0 ± 0.0	0.1
Augaptilus glacialis			0.0 ± 0.0	0.0
Bradyidius similis C4–C6	3.6 ± 8.6	50.6	0.6 ± 3.0	26.4
Calanus finmarchicus	155.2 ± 89.3	415.9	456.7 ± 578.9	3331.8
Calanus glacialis	103.1 ± 94.9	408.8	91.6 ± 92.3	437.8
Calanus hyperboreus	12.8 ± 16.5	111.5	8.4 ± 10.8	69.5
Chiridius obtusifrons C4–C6	0.0 ± 0.0	0.0	0.0 ± 0.1	0.8
<i>Copepoda</i> nauplii	107.3 ± 126.3	583.9	68.9 ± 77.7	496.4
Disco sp. C4–C6			0.0 ± 0.0	0.1
Gaetanus brevispinus C4–C6			0.0 ± 0.0	0.4
Gaetanus tenuispinus C4–C6	0.0 ± 0.1	0.4	0.0 ± 0.1	1.0
Harpacticoida	1.0 ± 3.0	20.3	0.3 ± 0.6	2.5
Heterorhabdus norvegicus	0.1 ± 0.3	2.0	0.1 ± 0.2	1.0
Mesaiokeras spitsbergensis	0.1 ± 0.2	1.2		
Metridia longa	21.5 ± 23.0	101.7	14.3 ± 13.9	73.2
Microcalanus spp.	31.4 ± 23.0	90.6	39.3 ± 31.5	242.2
Microsetella norvegica	0.0 ± 0.0	0.1	0.1 ± 0.2	1.1
Monstrilloida indet. C6F	0.0 ± 0.1	0.7	0.0 ± 0.1	0.4
Neomormonilla minor C5–C6			0.0 ± 0.0	0.3
Neoscolecithrix farrani C4–C6	0.2 ± 1.3	8.8	0.0 ± 0.1	1.0
Oithona atlantica C5–C6	7.9 ± 10.0	38.5	16.8 ± 24.0	194.1
Oithona similis	666.5 ± 786.1	3927.5	560.6 ± 593.7	3419.9
Oncaea parila C6F			0.0 ± 0.0	0.4
Oncaea spp. C6F			0.5 ± 3.7	35.6
Paraeuchaeta barbata C6	0.0 ± 0.0	0.0	0.0 ± 0.0	0.4
Paraeuchaeta glacialis C6	0.0 ± 0.0	0.0	0.0 ± 0.1	0.8
Paraeuchaeta norvegica C6	0.0 ± 0.0	0.1	0.0 ± 0.1	0.6
Paraeuchaeta spp. C1–C5	0.1 ± 0.2	0.9	0.5 ± 0.8	3.8
Paraheterorhabdus			0.0 ± 0.0	0.0
compactus C4–C6				
Pleuromamma robusta C6F	0.0 ± 0.0	0.1	0.0 ± 0.1	0.4
Pseudocalanus acuspes C6F	15.5 ± 26.6	135.7	3.8 ± 6.8	47.8
Pseudocalanus minutus C6F	3.5 ± 5.0	29.8	3.7 ± 5.2	33.3

(continued)

	1996–2006		2007-2016	
	All stations		All stations	
Copepoda	Mean ± StDev	Max	Mean ± StDev	Max
Pseudocalanus spp. C1-C5, C6M	268.3 ± 462.5	2314.4	158.5 ± 161.0	855.1
Pseudochirella spectabilis C4-C6			0.0 ± 0.0	0.0
Rhincalanus nasutus C4-C6			0.0 ± 0.0	0.4
Scaphocalanus brevicornis			0.0 ± 0.0	0.4
Scaphocalanus magnus			0.0 ± 0.0	0.1
Scolecithricella minor	0.1 ± 0.2	0.6	0.3 ± 0.4	1.9
Spinocalanus antarcticus			0.0 ± 0.0	0.2
Spinocalanus horridus C4–C6			0.0 ± 0.0	0.4
Spinocalanus longicornis C6			0.0 ± 0.0	0.2
Spinocalanus spp. C1-C6	0.0 ± 0.0	0.0	0.0 ± 0.1	0.4
Temorites brevis			0.0 ± 0.0	0.0
Tharybidae indet. C4–C6			0.0 ± 0.1	0.4
Tharybis groenlandicus C6			0.0 ± 0.0	0.0
Triconia borealis C6	5.0 ± 11.4	62.6	20.4 ± 27.7	216.4
Triconia conifera C6F	0.0 ± 0.0	0.0	0.0 ± 0.1	0.8
Triconia/Oncaea spp. C1-C5	0.1 ± 0.3	1.6	0.1 ± 0.3	1.6
Undinella oblonga C4–C6			0.0 ± 0.0	0.0
Xantharus siedleckii	0.0 ± 0.1	0.4	0.0 ± 0.0	0.2

Table 7.3 (continued)

Missing values indicate zero occurrences, while values marked 0.0 mean <0.04 ind. m⁻³

Pseudocalanus spp. is generally higher in the centre of the fjord than at stations further out (Table 7.5; Walkusz et al. 2009). The biomass contribution of *Pseudocalanus* spp. to the zooplankton size fraction, ranging from 0.2 to 10 mm, was estimated to 2% during summer-early autumn (Ormanczyk et al. 2017).

A mixture of three Pseudocalanus species (P. minutus, P. acuspes and P. moultoni) co-occurs in Kongsfjorden, and their proportion depends on environmental conditions (Aarbakke et al. 2017). Pseudocalanus minutus dominated during 2005–2009, although not in 2004 when about 50% of the specimen found were P. acuspes (Aarbakke et al. 2017). The share of P. moultoni varied between about 5% and 25%, although this species was not present in 2007. Pseudocalanus minutus and P. moultoni are more oceanic species associated with Atlantic Water, while P. acuspes is a coastal/shelf species associated with cold Arctic Water that is subject to mixing processes on the shelf (Cottier et al. 2005). The species composition may vary seasonally with dominance of P. minutus during spring and P. acuspes during summer and autumn in 2002 (Walkusz et al. 2009). Pseudocalanus moultoni was for the first time recorded in Kongsfjorden in summer 2004, based on molecular techniques (Aarbakke et al. 2017). However, the majority of studies present abundance or biomass data for Pseudocalanus at the genus level because of difficulties in identification of individuals for the entire size- and age spectrum based on morphology.

Pseudocalanus minutus has a 1-year life cycle in Kongsfjorden with reproduction taking place in May/June. During this time, adult females and males represent a significant share on the total population. The dominant overwintering stages are copepodids C3, C4, and C5 (Lischka and Hagen 2005). According to the lipid signature, *P. minutus* is an opportunistic feeder with predominance for herbivore nutrition exploiting the diatom bloom in spring and changing to a flagellate-based diet during summer-autumn, and omnivorous/carnivorous low-level feeding during winter (Lischka and Hagen 2007; Lischka et al. 2007). This species uses lipid deposits (wax esters) to develop into copepodid stages C3 and C4 in summer/autumn and for gonad maturation in C5 and females during the dark season. Final gonad maturation and reproduction seem to depend on the spring phytoplankton bloom (Lischka and Hagen 2007; Lischka et al. 2007). Whether or not *P. acuspes* successfully reproduces in Kongsfjorden is unclear (Lischka and Hagen 2005), and little is known about *P. moultoni* in the fjord, except that it is present (Aarbakke et al. 2017).

7.3.3 Calanus

Calanoid copepods of the genus *Calanus* dominate the mesozooplankton community in Kongsfjorden in terms of biomass (Fig. 7.5; Kwasniewski et al. 2003; Walkusz et al. 2009). The populations of the Atlantic *Calanus finmarchicus* and the Arctic *C. glacialis* in Kongsfjorden consist of local and advected individuals, with the proportions of each varying annually (Table 7.5). The relative abundances of *C. finmarchicus* and *C. glacialis* in Kongsfjorden likely depend on the timing and volume of Atlantic and Arctic water intrusions and, thus, on the inflow of Atlantic Water (Tverberg et al., Chap. 3). The larger *C. hyperboreus*, which is a deep-water species (Hirche 1997), was only present in low numbers in Kongsfjorden and does not contribute much to the total abundance of *Calanus* (Table 7.5).

Calanus spp. have been extensively studied in Kongsfjorden (Kwasniewski et al. 2003; Walkusz et al. 2009; Daase et al. 2013; Kwasniewski et al. 2013). A 1-year life cycle has been suggested for *C. finmarchicus* (Kwasniewski et al. 2003), while *C. glacialis* may need 1–2 years to fulfil its life cycle (Daase et al. 2013). Seasonal accumulation of lipid stores is linked to the different life strategies of *C. finmarchicus*, *C. glacialis* and *C. hyperboreus* (Scott et al. 2000; Falk-Petersen et al. 2009). *Calanus* spp. conduct seasonal vertical migrations with descent to overwintering depth taking place at the end of the summer. In Kongsfjorden, the majority of the population is usually found at depth by the end of July and in August, although the timing may vary among years (Kwasniewski et al. 2003; Walkusz et al. 2009; Daase et al. 2013). The overwintering populations remain at depth during autumn and early winter. Recent studies during the polar night have shown that the ascent from overwintering depth occurs much earlier than previously assumed, and both *C. finmarchicus* and *C. glacialis* are distributed all over the water column as early as late

January or early February (Daase et al. 2014; Berge et al. 2015a, b; Grenvald et al. 2016). The early spring population is dominated by females and overwintering stages (C4 and C5), and the new generation appears before or during the spring bloom and develops rapidly over the summer (June and July) to overwintering stages (Walkusz et al. 2009; Daase et al. 2013). Reproductive strategies vary between C. finmarchcius and C. glacialis, with the latter being able to mature and reproduce eggs prior to the spring bloom based on its large lipid stores (capital breeding; Varpe 2012). Thus, females of C. glacialis are abundant prior to the spring bloom and young copepodids are already present at the onset of the bloom (Daase et al. 2013). Energy reserves accumulated for overwintering become depleted in C. finmarchicus and, therefore, this species relies on the spring bloom for reproduction (income breeding; Varpe et al. 2009). As a result, the new generation appears later than that of C. glacialis. These differences in reproductive strategies may explain the high variability in C. finmarchicus abundance in Kongsfjorden (Table 7.3; Kwasniewski et al. 2003). Calanus glacialis shows high flexibility in reproductive strategies as an adaptation to the environmental constraints of Arctic shelf seas (Daase et al. 2013) and may be more successful to reproduce under high-Arctic conditions than C. finmarchicus. The relatively stable abundance of C. glacialis in Kongsfjorden indicates the presence of a local population, while the high variability in C. finmarchicus indicates that the population is likely maintained by both local and advected individuals (Kwasniewski et al. 2003).

7.3.4 Amphipods

Amphipods show large spatial and temporal variability, with higher abundances in the innermost part of the fjord (Fig. 7.6; Dalpadado et al. 2016). The inner part is dominated by the Arctic Themisto libellula and the outer parts by the boreal-Atlantic T. abyssorum (Dalpadado et al. 2016; Legeżyńska et al. 2017). The Arctic species typically has higher abundance and biomass during cold year, whereas T. abyssorum is more abundant during warm periods (Hop et al. 2006). Three cohorts of T. libellula have been recorded in Kongsfjorden, and this species likely has two spawning seasons (March-April) in the fjord within their 3-year life span (Dale et al. 2006). As a carnivore species, its growth pattern is similar to carnivorous krill, M. norvegica, which feed throughout the winter (Falk-Petersen 1985). The life span of T. abyssorum was found to be 1 year in the Norwegian Sea, and 2 years in European Arctic seas (Koszteyn et al. 1995). Ice-associated amphipods, such as Apherusa glacialis and Gammarus wilkitzkii are occasionally found in Kongsfjorden (Table 7.2). Their occurrence is most probably associated with presence of drifting sea ice in the fjord or on the adjacent shelf, and, thus, their low abundance during summer (Table 7.4) reflects the recent decline in sea ice.



Fig. 7.6 Changes in biomass of copepod species over time, based on MultiNet samples (200 μm mesh size) from 1996–2016. Coloured bars indicate average biomass for each year using stations as statistical replicates. Error bars represent bootstrapped 95% confidence intervals (CIs) for the means. Missing error bars indicate values with only one replicate (e.g. one station). Error bars that reach all the way down to zero represent negative minimum CIs indicating low confidence for the mean estimate. Species that indicated changes over time in the RDA (Fig. 7.10) were selected for the figure

7.3.5 Euphausiids

Recent population studies on Kongsfjorden krill have focused on growth and reproduction and are accompanied by eco-physiological investigations, i.e. energy storage and turnover measurements including experimentation on thermal and trophic requirements (Huenerlage and Buchholz 2015; Huenerlage et al. 2016). During the last decades, the species composition of krill has changed due to recent increased advection of Atlantic water masses carrying characteristic boreal as well as

	1996-2006		2007-2016	
	All stations		All stations	
Taxa	Mean ± StDev	Max	Mean ± StDev	Max
Amphipoda				
Amphipoda indet.	0.0 ± 0.0	0.1	0.0 ± 0.1	0.4
Apherusa glacialis			0.0 ± 0.0	0.4
Cyclocaris guilelmi			0.0 ± 0.0	0.0
Eusirus holmii			0.0 ± 0.0	0.4
Hyperia galba	0.0 ± 0.0	0.0		
Hyperiidae indet.	0.0 ± 0.0	0.0		
Hyperoche medusarum	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0
Onisimus spp.	0.0 ± 0.0	0.0		
Scina borealis			0.0 ± 0.0	0.4
Themisto abyssorum	0.7 ± 0.7	4.0	1.1 ± 1.2	7.7
Themisto libellula	0.7 ± 1.8	9.4	0.3 ± 0.4	1.6
Euphausiacea				
Euphausiacea indet. (larvae)	0.1 ± 0.1	0.6	0.6 ± 0.8	4.7
Meganyctiphanes norvegica	0.0 ± 0.0	0.1	0.0 ± 0.0	0.0
Thysanoessa inermis	0.0 ± 0.1	0.4	0.3 ± 0.6	4.0
Thysanoessa longicaudata	0.1 ± 0.2	0.9	0.0 ± 0.1	0.8
Thysanoessa raschii	0.1 ± 0.8	5.7	0.3 ± 2.4	23.2
Other Crustacea				
Bopyridae indet.	0.0 ± 0.3	1.9	0.6 ± 0.8	4.6
Boreomysis arctica	0.0 ± 0.0	0.0	0.0 ± 0.0	0.1
Cumacea indet.	0.0 ± 0.0	0.2	0.0 ± 0.0	0.4
Eusergestes arcticus			0.0 ± 0.0	0.0
Evadne nordmanni	0.5 ± 3.3	24.2	1.2 ± 11.0	104.7
Facetotecta indet.	0.1 ± 0.4	1.9	0.4 ± 0.7	3.7
Hymenodora glacialis	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0
Isopoda indet.	0.2 ± 0.2	1.1	0.1 ± 0.2	1.5
Mysidae indet.	0.0 ± 0.0	0.0		
Ostracoda indet.	0.6 ± 2.6	19.1	0.5 ± 0.8	4.5
Pseudomma truncatum	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0
Tanaidacea indet.	0.0 ± 0.0	0.0		
Meroplankton				
Bivalvia larvae and juveniles	166.7 ± 595.6	4188.9	130.8 ± 310.8	1887.6
Bryozoa larvae	0.1 ± 0.3	1.6	0.1 ± 0.3	2.3
Cirripedia nauplii and cyprid	1.5 ± 4.2	22.9	2.4 ± 9.8	81.5
Decapoda larvae	0.1 ± 0.4	2.7	0.0 ± 0.0	0.5
Echinodermata larvae	114.5 ± 274.5	1244.8	39.7 ± 55.3	248.6

Table 7.4 Abundance (ind. m⁻³) of other taxa than copepods in Kongsfjorden during the periods 1994–2006 and 2007–2016, averaged over all sampled stations and based on MultiNet samples

(continued)

	1996-2006		2007-2016	
	All stations		All stations	
Taxa	Mean ± StDev	Max	Mean ± StDev	Max
Gastropoda larvae	0.1 ± 0.2	0.9	2.7 ± 20.9	199.4
Hyas araneus	0.0 ± 0.1	0.4	0.0 ± 0.1	1.0
Nemertea pilidium	0.0 ± 0.1	0.5	0.0 ± 0.1	0.3
Pagurus pubescens	0.0 ± 0.1	0.9	0.1 ± 0.2	1.5
Pandalus borealis	0.0 ± 0.0	0.1	0.0 ± 0.1	0.7
Polychaeta larvae	4.3 ± 8.2	42.1	1.9 ± 2.3	15.3
Sabinea septemcarinata	0.0 ± 0.1	0.6	0.0 ± 0.1	0.5
Typhloscolecidae larvae			0.0 ± 0.1	0.8
Cnidaria				!
Aeginopsis laurentii	0.0 ± 0.0	0.0	0.0 ± 0.0	0.2
Aglantha digitale	0.4 ± 0.9	6.1	0.5 ± 1.3	10.7
Botrynema ellinorae			0.0 ± 0.1	0.8
Bougainvillia spp.			0.0 ± 0.0	0.1
Dimophyes arctica	0.0 ± 0.0	0.2	0.0 ± 0.1	0.8
Halitholus cirratus	0.0 ± 0.0	0.0	0.0 ± 0.0	0.1
Hydrozoa indet.	0.0 ± 0.0	0.1	0.0 ± 0.2	0.8
Nanomia cara			0.0 ± 0.0	0.0
Sarsia sp.	0.0 ± 0.0	0.2		
Scyphozoa indet.			0.0 ± 0.0	0.2
Siphonophora indet.	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0
Ctenophora				
Beroë cucumis	0.3 ± 0.8	6.1	0.1 ± 0.1	1.0
Ctenophora			0.0 ± 0.1	0.6
Mertensia ovum	0.1 ± 0.4	2.8	0.1 ± 0.5	4.3
Pteropoda				!
Clione limacina	4.5 ± 25.9	187.8	0.5 ± 3.6	34.6
Limacina helicina	3.3 ± 6.5	27.3	73.8 ± 282.8	2277.5
Limacina retroversa	0.1 ± 0.1	0.6	0.1 ± 0.3	2.6
Annelida				
Pelagobia sp.	0.0 ± 0.0	0.3	0.0 ± 0.1	0.8
Tomopteris helgolandica			0.0 ± 0.0	0.1
Tomopteris spp.	0.0 ± 0.0	0.2		
Chaetognatha				
Eukrohnia hamata	2.0 ± 1.9	9.1	2.5 ± 2.8	15.5
Parasagitta elegans	3.5 ± 6.1	41.4	2.1 ± 2.4	11.8
Pseudosagitta maxima			0.0 ± 0.0	0.0
Appendicularia	I			
Appendicularia			0.0 ± 0.0	0.1
Fritillaria borealis	26.5 ± 47.4	250.3	10.5 ± 19.0	90.9
Oikopleura spp.	2.8 ± 4.1	21.5	6.3 ± 16.2	131.4
Pisces	0.0 ± 0.0	0.1	0.0 ± 0.0	0.1

Table 7.6 (continued)

Missing values indicate zero occurrences, while values marked 0.0 mean <0.04 ind. m⁻³

subtropical-boreal euphausiids into the ecosystem (Buchholz et al. 2010; Dalpadado et al. 2016). Concurrently, the temperate-boreal (Meganyctiphanes norvegica) and subtropical-temperate krill species (Nematoscelis megalops) are regularly found, at low abundances, in Kongsfjorden - in addition to the previously prevailing Arctoboreal coastal species T. inermis and T. raschii and oceanic species T. longicaudata (Buchholz et al. 2010). A comparison of nutrition and energy storage strategies, stable isotopes, lipid profiles and fatty acid compositions have shown remarkable differences between the krill species. Thysanoessa inermis and T. longicaudata typically consist of 30-50% lipids of dry mass, mainly stored as triacylglycerols and wax esters, with fatty acids indicating herbivorous feeding (Sargent and Falk-Petersen 1981). This large lipid store may have multiple functions, including winter survival when food sources are low. On the other hand, M. norvegica and N. megalops appear more carnivorous, with significantly lower mean lipid contents (29 and 10%, respectively) and different energy storage patterns (triacylglycerols and polar lipids, respectively; Huenerlage et al. 2016). Top predators relying on krill as a food source (e.g. Vihtakari et al. 2018) may therefore be exposed to krill species of less quality in their diet.

Thysanoessa raschii was observed spawning for the first time in Kongsfjorden in 2011 (Buchholz et al. 2012; Huenerlage and Buchholz 2015; Huenerlage et al. 2015). Respiration measurements revealed *Thysanoessa* spp. to appear more cold-stenotherm than the other krill species: the upper level of respiratory capacity is reached at 12 °C (K. Huenerlage and F. Buchholz, unpubl.). Thus, thermal stress may have caused the decline after 2011. In contrast, the other temperate-boreal and the subtropical-temperate krill species show higher tolerance to temperature changes, which may explain their recent success with northward expansion.

Krill is probably highly underestimated by all nets used for sampling in Kongsfjorden (Pearcy et al. 1983). A distinct acoustic back scattering layer of krill was recorded with an Acoustic Zooplankton and Fish Profiler with consistent dial vertical migration from surface to 150 m from January to March 2014. High biomass was recorded in June 2014 with 3.2 g m⁻² and in January with > 0.6 g m⁻² (Grenvald et al. 2016; Darnis et al. 2017). During a cruise to Kongsfjorden in January 2014, Larsen (2017) recorded very high abundance of krill (mainly *T. inermis*) with 60,000–120,000 krill per 15-min trawl haul with "Harstad" pelagic trawl (20 × 20 m mouth opening, 8 mm cod-end mesh size). *Thysanoessa inermis* was also by far the dominating food for Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), and polar cod (*Boreogadus saida*) in January 2014–2016 with a frequency of occurrence in the stomach of 25–50%, while only mediumsized polar cod had copepods as the main food, accounting for 40% (Larsen 2017).

Krill are typically associated with underwater slopes or deep troughs (e.g. 100–200 m slope in front of Ny-Ålesund; 95 m depression in inner fjord), where they feed on the rich nepheloid layer (Buchholz et al. 2010). Bottom topography plays a role for krill aggregations: a minimum water depth of ca. 60 m is typically required to allow for vertical migration or positioning (Falk-Petersen and Hopkins 1981; Falk-Petersen and Kristensen 1985). In April 2013, the highest concentration of krill was 270 ind. m⁻³ near the bottom at 250–300 m depth in mid-fjord (near Kb3; F. Buchholz unpubl. data).

7.3.6 Ctenophores and Other Gelatinous Zooplankton

Gelatinous predators such as ctenophores, hydromedusae, siphonophores and scyphomedusae, can be quite abundant in the Arctic, but relatively little is known about their biology since they are difficult to collect and preserve (e.g. Raskoff et al. 2005, 2010; Purcell et al. 2010). They feed partly on the lower pelagic food web and can be important regulators of zooplankton in the Arctic (Purcell 1991; Swanberg and Båmstedt 1991; Majaneva et al. 2013).

Two ctenophore species are commonly observed in Kongsfjorden: Mertensia ovum and Beroë cucumis (Table 7.4; Lundberg et al. 2006; Majaneva et al. 2013). Mertensia ovum can dominate the gelatinous zooplankton community in Kongsfjorden accounting for up to 70% of the abundance (Hop et al. 2002). Mertensia ovum is an opportunistic feeder preying mainly on the large Calanus copepods (Falk-Petersen et al. 2002; Majaneva et al. 2013) but also on smaller copepods, pteropods and fish larvae (Swanberg and Båmstedt 1991; Siferd and Conover 1992; Purcell et al. 2010). Peak abundance of *M. ovum* has been found during summer in Kongsfjorden and was likely related to increased zooplankton abundance at the same time (Lundberg et al. 2006). Mertensia ovum has special storage structures for lipids originating from their Calanus diet (Larson and Harbison 1989; Falk-Petersen et al. 2002), with highest lipid content during autumn (Lundberg et al. 2006; Graeve et al. 2008). Lipids are likely used to fuel prolonged periods of reproduction enabling their 2-years life cycle in Kongsfjorden (Lundberg et al. 2006). The population of *M. ovum* is mainly controlled by another Arctic ctenophore species, Beroë cucumis (Swanberg 1974; Tamm and Tamm 1991). Ctenophores are preved upon by higher trophic levels, such as polar cod, Atlantic cod and sea birds, although the gelatinous masses are difficult to identify in stomach contents of a mixed diet.

7.3.7 Chaetognaths

While most zooplankton studies from Kongsfjorden have focused on copepods, euphausiids or ctenophores, little is known about the chaetognath population in Kongsfjorden despite them being one of the most abundant and consistently present carnivorous zooplankton species (Table 7.4). Chaetognaths form a phylum of pelagic predators that can comprise 7–18% of zooplankton biomass in the Arctic (Kosobokova et al. 1998; Kosobokova and Hirche 2000; Hopcroft et al. 2005). The two chaetognath species found in Kongsfjorden are commonly found in Svalbard waters and across the Arctic (Søreide et al. 2003; Hopcroft et al. 2005). *Eukrohnia hamata* is usually associated with open water, while *Parasagitta elegans* dominates in the fjords (Dunbar 1962; Welch et al. 1996; Kosobokova et al. 2011). *Parasagitta elegans* was the only chaetognath species observed in seasonal studies in Kongsfjorden (Walkusz et al. 2009; Lischka and Hagen 2016). This species dominated in numbers over *E. hamata* during winter (January–February) in Kongsfjorden

(Grenvald et al. 2016). Chaetognaths prey on copepods and other zooplankton species (Solov'ev and Kosobokova 2003; Terazaki 2004; Grigor et al. 2015). They may contain high amounts of lipids (Kruse et al. 2010) and are prev items for larger zooplankton, fish and seabirds (Feigenbaum and Maris 1984), although little is known on their importance as prev in Kongsfjorden. Highest chaetognath abundance is usually observed in summer and autumn (Grigor et al. 2014). Lischka and Hagen (2016) found peak abundance of chaetognaths in Kongsfjorden in November, while Grenvald et al. (2016) observed considerable higher abundance of *P. elegans* in January 2013 and 2014 (342-701,000 ind. m⁻³) than in February 2013 (16,000-26,000 ind. m^{-3}). The life cycle of *P. elegans* is estimated to be 3 years in Svalbard fjords (Grigor et al. 2014), although both species had longevities of about 2 years in the Canadian Arctic Ocean (Grigor et al. 2017). Parasagitta elegans displays signs of ontogenetical vertical migration, with younger individuals distributed shallower and larger/older ones deeper (Grigor et al. 2014). This species has also shown signs of diel vertical migration (DVM) behaviour in February in Kongsfjorden (Grenvald et al. 2016).

7.3.8 Pteropods

The pteropod *Limacina helicina* is an important member of the zooplankton community in the Arctic, and high densities have been found in the Greenland Sea, the area around Svalbard and in the northern Barents Sea (Gilmer and Harbison 1991; Falk-Petersen et al. 1999). It is abundant in Kongsfjorden year-round (Weslawski et al. 2000; Lischka and Hagen 2016), but appeared only in pulses of low density during a study by Gannefors et al. (2005), which might be due to their patchy distribution (Kerswill 1940) and inter-annual variability in population dynamics. Aggregations of adult *L. helicina* can frequently be observed in Kongsfjorden during the period of reproduction in summer when they appear close to the surface drifting with the currents across the fjord while feeding, but they are difficult to sample quantitatively (Gannefors et al. 2005). In our time series data, we observed high variability in abundance of veligers, which are more efficiently caught with the MultiNet compared to adults (Table 7.6). The winter abundance is variable, and may be orders of magnitude higher some years, such as the winter 1998/99 (Lischka and Riebesell 2012; Lischka and Hagen 2016).

Limacina spp. have delicate shells made of aragonite that easily dissolves when the aragonite saturation state (Ω_{Ar}) approaches 1 (Lischka et al. 2011; Bednaršek et al. 2014). Studies performed in Kongsfjorden have reported occurrences of critical Ω_{Ar} levels <1 in winter (February 2010) (Lischka and Riebesell 2012) and of declining Ω_{Ar} gradients towards the inner fjord, where the freshwater input is the largest, with low values of 1.5 (Fransson et al. 2016). Thus, *L. helicina* may be affected by combined effects of ocean acidification (OA) and increased temperature in Kongsfjorden, which has also been indicated by experimental work (e.g. Comeau et al. 2009; Lischka et al. 2011). The subarctic boreal species *Limacina retroversa* is probably introduced to Kongsfjorden with advected AW (e.g. Hop et al. 2006). The importance of *L. retroversa* in the eastern Fram Strait and also in Kongsfjorden has increased since 2005/06 due to an increased influence of warmer Atlantic water masses (Lischka and Riebesell 2012; Bauerfeind et al. 2014), although we do not see a similar signal in our time-series data comparing 1996–2006 to 2006–2016 (Table 7.4). The occurrence and abundance of this species could be used as an indicator of increasing influence of warm AW in Kongsfjorden and adjacent seas (Lischka and Riebesell 2012; Lischka and Hagen 2016).

Pteropod studies in Kongsfjorden have included both the thecosmes (shell-bearing) *L. helicina* and *L. retroversa* and also the gymnosome *Clione limacina*. Studies have covered aspects of the species life cycles and their lipid dynamics (Falk-Petersen et al. 2001; Böer et al. 2005; Gannefors et al. 2005) as well as of the potential vulnerability of *L. helicina* and *L. retroversa* to OA and warming (Comeau et al. 2009; Lischka et al. 2011; Lischka and Riebesell 2012, 2017).

Limacina helicina has a 1-year life cycle in Kongsfjorden, and reproduction takes place during the summer months (June–August) with a peak usually in August (Gannefors et al. 2005). The veliger larvae make use of the summer phyto-/proto-zooplankton bloom and develop to juveniles prior to overwintering at reduced metabolic rates. Further development ceases until the next spring when overwintering juveniles continue development into adults using the spring phytoplankton bloom (Gannefors et al. 2005; Lischka and Riebesell 2012, 2017; Lischka and Hagen 2016). The other pteropod *Clione limacina* has a life-cycle of at least 2 years in Svalbard waters. Polytrochous larvae occur in April/May and develop to adults until summer. From September through winter, almost only mature adults with large lipid stores can be found and they feed predominately on *L. helicina* (Böer et al. 2005).

The role and impact of *L. helicina* on the pelagic food web of Kongsfjorden is currently not defined, but can be assumed substantial during spring and summer when *Limacina* develops rapidly from overwintering juveniles to reproducing adults. This species can become extremely abundant, as observed in Rijpfjorden, northern Svalbard, where up to 8000 m⁻³ juveniles were recorded to perform diel vertical migrations in the upper 50 m (Falk-Petersen et al. 2008). In the Southern Ocean, the grazing impact of *L. retroversa* can account for up to 60% of the total plankton production (Hunt et al. 2008).

7.3.9 Appendicularians

Appendicularians (Larvacea) can appear in high abundances in Kongsfjorden (Walkusz et al. 2009; Lischka and Hagen 2016). However, like chaetognaths, appendicularians have not specifically been studied in Kongsfjorden and little is known

about this group, species life cycles and their role in the ecosystem. Appendicularians ingest nano- and picoplankton with high efficiency (Acuna et al. 1999, 2002) and mediate the export of these cells from the euphotic layer to the sea floor through the sinking of faecal pellets and discarded mucous houses, which enhance forming of aggregates and the downward vertical fluxes of particles. Representatives of two genera of larvaceans occur in Kongsfjorden, Fritillaria represented by F. borealis, and Oikopleura, with possibly two species O. vanhoeffeni and O. labradoriensis. Fritillaria borealis typically was more abundant than Oikopleura spp. in July. High numbers of F. borealis in Fram Strait and the Barents Sea have been associated with Atlantic waters (Arashkevich et al. 2002; Blachowiak-Samolyk et al. 2017). Appendicularians can appear in high abundance for short periods. Such outbursts have been related to high fecundity and growth rates resulting in short generation time (days rather than weeks), as well as rapid population growth in response to bacterio- and nanophytoplankton blooms (Hopcroft and Roff 1995). During outappendicularians can dominate the mesozooplankton community bursts, (Arashkevich et al. 2002). In Kongsfjorden, peak abundances of F. borealis have been observed in July (Lischka and Hagen 2016), when they can contribute 2.7% of the total zooplankton abundance, although their abundance in July vary substantially among years (0-6.9%; Hop et al. 2006). Peak abundance of Oikopleura spp. has been observed in June in Kongsfjorden (Lischka and Hagen 2016). A similar decoupling of abundance peaks between the two appedicularian species has been observed in Rijpfjorden (Weydmann et al. 2013) as well as in the northeastern Chukchi Sea (Questel et al. 2013).

7.3.10 Meroplankton

The occurrence of meroplankton is highly seasonal and outbursts are often restricted to a few weeks during and after the spring bloom. They often occur at the same time as copepod nauplii (Kwasniewski et al. 2013). Studies from Kongsfjorden (Lischka and Hagen 2016) and Adventfjorden (Kuklinski et al. 2013; Stübner et al. 2016) have shown that different meroplankton taxa appear in repeatable sequences, with cirripedia nauplii and polychaete larvae being the first to appear, usually in May–June and occasionally as early as April (Walkusz et al. 2009), then followed by bivalves and echinoderms later in the summer. Mass appearance of cirripede nauplii have been reported during spring (Kwasniewski et al. 2013), whereas Echinodermata larvae might play an important role during summer as they swarm in surface waters (Walkusz et al. 2009). Juvenile bivalves and echinoderms were the dominating meroplanktonic taxa in our time-series data from mid-end July (Table 7.6). Meroplankton were particularly abundant in 2006 in inner fjord, and also partly in 2007 in mid-fjord.

7.3.11 General Seasonality Patterns in the Zooplankton Community

The extreme seasonality in incoming solar radiation and primary production lead to pronounced seasonal variations in zooplankton abundance at high latitudes. Zooplankton abundance peaks are usually observed in late summer and autumn, while abundance minima occur in early spring. This has been commonly observed in Kongsfjorden (e.g. Willis et al. 2006; Walkusz et al. 2009; Lischka and Hagen 2016) and other fjords in Svalbard (e.g. Weslawski et al. 1988; Arnkværn et al. 2005; Weydmann et al. 2013). The zooplankton abundance can be an order of magnitude higher during summer and autumn than in spring in Kongsfjorden, when C. finmarchicus, O. similis and Calanus nauplii dominate the zooplankton community (Walkusz et al. 2009). Recent zooplankton studies performed during the polar night have shown that small copepods (Microcalanus, O. similis, Pseudocalanus) dominated in January in Kongsfjorden (Berge et al. 2015a; Grenvald et al. 2016), when they were present in similar abundance (400-1200 ind. m⁻³) as observed in our time series data from July, while larger zooplankton were generally much less abundant than during the other seasons (Berge et al. 2015a). The reasons and range of zooplankton activity observed during the dark season in Kongsfjorden have been discussed by Berge et al. (2015b).

Advection of Atlantic Water during summer can cause increased abundances of *C. finmarchicus* relative to Arctic species (Willis et al. 2006; Walkusz et al. 2009). *Calanus glacialis* abundances are usually also highest in summer and autumn, at the end of the productive period, especially inside the fjord, where the Arctic species can find refugia in the deepest parts of the fjord basin in cold bottom water (Walkusz et al. 2009).

Many of the zooplankton species in Kongsfjorden perform diurnal vertical migrations, but the pattern varies between seasons from very pronounced DVM during spring and autumn, which continues to some extent during winter (Berge et al. 2009), although being absent or asynchronous DVM during summer with 24 h day-light (Cottier et al. 2006; Wallace et al. 2010). These changes will then also influence where in the water column most of the biomass is located during the day over seasons, typically shallow in connection with the plankton blooms during spring and summer and deeper during late autumn and winter (Walkusz et al. 2009).

7.3.12 Pelagic Food Web and Vertical Flux

Zooplankton have important functions in the pelagic ecosystem of Kongsfjorden, where they occupy the second and third trophic levels in the marine food web (Hop et al. 2002). The secondary production by zooplankton at the second and third trophic level has been quantified as 0.13-5.69 g C m⁻² year⁻¹ (Duarte et al., Chap. 12). They represent important grazers in the system and with 10× greater standing stock

than the phytoplankton during summer, they can exert top-down control on the primary production (Hegseth et al., Chap. 6). Faecal pellet from zooplankton constitute a major contribution to the vertical flux (Wassmann et al. 1991, 1996), with higher sedimentation during summer because of the high grazing activity due to higher zooplankton abundance and biomass. Darnis et al. (2017) recently estimated, based on sediment traps, that DVM-mediated carbon transport by krill and copepods represent >25% of the POC flux during the first weeks of autumn and > 40% of during winter.

7.4 Part II: Trends in the Zooplankton Time-Series

7.4.1 Zooplankton in General and Calanus in Particular

Annual monitoring of mesozooplankton over the last 20 years since 1996 has shown that Kongsfjorden hosts a larger zooplankton biomass within the fjord compared to the stations outside Kongsfjorden (Fig. 7.5). The average biomass (mg dry mass m⁻³) differed significantly among the four areas; inner basin, outer basin, shelf and Fram Strait (Kruskal-Wallis df = 3, χ^2 = 36.5, p < 0.001). The average biomass in Fram Strait stations was significantly lower compared to other stations (Kruskal-Wallis multiple comparison). Biomass was highest in the inner basin with an average of 150 mg dry mass m⁻³. The copepods *C. glacialis* and *C. finmarchicus* contributed approximately 63.3% to the total biomass of inner and outer fjord (Fig. 7.5). *Calanus glacialis* contributed more to the total biomass in the inner and outer basin than *C. finmarchicus*, while the pattern was the opposite at the shelf and Fram Strait stations. The highest integrated biomasses in the water column (mg dry mass m⁻²) were encountered in outer basin and shelf stations, which are 2–3 times deeper than the inner basin stations (224–352 m at V12-Kb1 vs. 64–96 m at Kb7-Kb5).

The changes in the zooplankton community from 1996 to 2016 were generally nonlinear and differed between stations inside and outside Kongsfjorden. Large variability in the values and the small number of replicate stations complicate the interpretation of the patterns. Nevertheless, an increase in abundance and biomass of *C. finmarchicus* in both the inner and outer basin is evident (Table 7.5 and Fig. 7.6). However, the trend is not continuous, as a decrease was observed in 2015–2016. Thus, it is unclear whether the increase represents a trend or merely fluctuations in the population size. A simultaneous decrease in *C. glacialis* was not observed.

High inter-annual variation in the contribution of different species both in terms of abundance (Tables 7.5 and 7.6) and biomass (Figs. 7.6 and 7.7) in different parts of Kongsfjorden likely relates to the variable inflow of Atlantic Water. The fluctuations in biomass of *Calanus* species appeared to loosely follow the estimated proportions of Arctic and Atlantic Water in the fjord (Fig. 7.2), whereas temporal changes in biomass

(from stage 1 to stage 6 female or male, C1–C6F/M, which contributed to the summary presented, are listed next to the species names. No stage indicates all copepodids C1–C6 are included Table 7.5 Total abundance (ind. m⁻³) of copepods in different areas of Kongsfjorden during the periods 1994–2006 and 2007–2016. The copepodid developmental stages

	1999–2006								2007-2016							
	Fram Strait		Shelf		Outer basin		Inner basin		Fram Strait		Shelf		Outer basin		Inner basiı	
Copepoda	Mean ± StDev	Max	Mean ± StDev	Max	Mean ± StDev	Max	Mean ± StDev	Max	Mean ± StDev	Max						
Acartia longiremis	0.0 ± 0.0	0			3.0 ± 6.3	38	20.7 ± 21.2	49.9	0.0 ± 0.2	0.6	1.9 ± 5.7	24.9	5.3 ± 6.5	27.1	7.4 ± 9.4	29
Aetideidae indet. C1–C3	0.0 ± 0.1	0.2	0.1 ± 0.1	0.2	0.8 ± 1.9	7.6	0.7 ± 1.9	5	0.2 ± 0.2	0.8	0.1 ± 0.3	0.9	1.7 ± 1.4	4.9	3.9 ± 4.1	15.9
Aetideopsis minor C4–C6	0.0 ± 0.1	0.1							0.0 ± 0.0	0.1			0.1 ± 0.9	5.9		
Aetideopsis rostrata C4-C6	0.0 ± 0.0	0							0.1 ± 0.1	0.4	0.0 ± 0.1	0.2	0.0 ± 0.0	0.3		
Aetideus armatus C4–C6					0.0 ± 0.0	0			0.0 ± 0.0	0	0.0 ± 0.0	0.1	0.0 ± 0.0	0.1		
Augaptilus glacialis									0.0 ± 0.0	0						
Bradyidius similis C4–C6	0.1 ± 0.1	0.2	0.0 ± 0.0	0.1	4.9 ± 9.9	50.6	1.6 ± 2.2	5.9					0.9 ± 4.2	26.4	1.1 ± 1.9	6.6
Calanus finmarchicus	115.8 ± 134.2	313.3	142.7 ± 80.9	267.7	151.1 ± 77.5	353	209.1 ± 123.8	415.9	67.1 ±53.0	185.6	381.2 ± 303.5	1191.8	444.6 ± 470.8	2115.2	866.2 ± 925.5	3331.8
Calanus glacialis	2.8 ± 2.7	6.6	101.9 ± 172.7	408.8	102.5 ± 80.0	332.3	164.4 ± 95.3	320.3	2.7 ± 2.6	9.3	57.5 ± 67.6	256.4	120.1 ± 87.0	400.3	133.4 ± 106.1	437.8
Calanus hyperboreus	0.5 ± 0.3	0.8	1.6 ± 2.0	5.1	11.2 ± 7.2	31.9	36.1 ± 35.0	111.5	1.7 ± 1.0	3.5	2.8 ± 3.5	15.7	12.5 ± 13.2	69.5	10.5 ± 9.6	34.2
Chiridius obtusifrons C4–C6	0.0 ± 0.0	0							0.1 ± 0.2	0.8	0.1 ± 0.2	0.7	0.0 ± 0.0	0.2		
Copepoda nauplii	47.2 ± 37.6	99.1	65.3 ± 86.1	209.5	76.3 ± 67.3	331.9	339.9 ± 184.8	583.9	23.5 ±28.2	107.8	119.5 ± 118.3	496.4	65.7 ± 60.5	282.2	57.9 ± 58.3	261.3

Disco sp. C4-C6									0.0 ± 0.0	0.1						
Gaetanus brevispinus C4–C6									0.0 ± 0.1	0.4						
Gaetanus tenuispinus C4–C6	0.2 ± 0.1	0.3	0.1 ± 0.2	0.4	0.0 ± 0.0	0	0.0 ± 0.1	0.3	0.2 ± 0.2	1	0.0 ± 0.1	0.4	0.0 ± 0.1	0.3		
Harpacticoida	0.0 ± 0.0	0.1	0.0 ± 0.0	0.1	0.3 ± 0.5	2.2	5.8 ± 6.9	20.3	0.0 ± 0.0	0	0.0 ± 0.1	0.3	0.3 ± 0.5	2.5	0.7 ± 0.9	2.5
Heterorhabdus norvegicus	0.8 ± 0.9	5	0.1 ± 0.1	0.2	0.0 ± 0.0	0.3			0.4 ± 0.2		0.1 ± 0.1	0.5	0.0 ± 0.1	0.3		
Mesaiokeras spitsbergensis					0.1 ± 0.2	1.2										
Metridia longa	3.7 ± 2.8	6.5	6.8 ± 5.8	16.7	28.8 ±23.8	101.7	2.7 ± 2.1	6.1	9.8 ± 4.0	17.3	10.2 ± 9.1	43	22.8 ± 15.6	73.2	3.5 ± 6.1	26.5
Microcalanus spp.	6.4 ± 7.2	16.7	9.8 ±11.7	24.2	36.3 ±21.1	82.5	34.5 ±28.7	90.6	23.2 ±6.3	29.9	43.4 ± 30.0	114	47.1 ±36.6	242.2	30.3 ± 27.2	116.3
Microsetella norvegica					0.0 ± 0.0	0.1			0.0 ± 0.0	0	0.1 ± 0.2	0.6	0.1 ± 0.2	1.1	0.2 ± 0.3	1.1
Monstrilloida indet. C6F					0.0 ± 0.1	0.7							0.0 ± 0.1	0.4		
Neomormonilla minor C5–C6									0.0 ± 0.1	0.2			0.0 ± 0.0	0.3		
Neoscolecithrix farrani C4–C6					0.0 ± 0.0	0.2	1.8 ± 3.3	8.8							0.1 ± 0.3	-
Oithona atlantica C5–C6	10.9 ± 16.5	35.6	7.4 ± 8.3	20.3	7.9 ± 9.5	38.5	6.7 ± 12.1	33.9	6.1 ± 4.0	14.1	22.8 ± 21.3	84.8	18.2 ± 29.9	194.1	15.7 ± 19.1	66.3
Oithona similis	151.5 ± 61.8	228.1	474.6 ± 209.6	715.2	492.3 ± 406.5	1702.8	2043.5 ± 1340.5	3927.5	87.7 ± 59.4	192.1	439.3 ± 258.8	1267.1	595.4 ± 607.9	3397.3	979.3 ± 745.4	3419.9
Oncaea parila C6F									0.0 ± 0.1	0.4						

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Table	

	1999–2006								2007-2016							
	Fram Strait		Shelf		Outer basin		Inner basin		Fram Strait		Shelf		Outer basin		Inner basi	
	Mean ±		Mean ±		Mean ±		Mean ±		Mean ±		Mean ±		Mean ±		Mean ±	
Copepoda	StDev	Max	StDev	Мах	StDev	Max	StDev	Max	StDev	Max	StDev	Max	StDev	Max	StDev	Max
Oncaea spp. C6F									0.2 ± 0.3	1.1	0.1 ± 0.2	0.6	1.0 ± 5.6	35.6	0.2 ± 0.5	2.2
Paraeuchaeta barbata C6			0.0 ± 0.0	0					0.0 ± 0.1	0.4	0.0 ± 0.0	0				
Paraeuchaeta glacialis C6	0.0 ± 0.0	0			0.0 ± 0.0	0			0.1 ± 0.2	0.8			0.0 ± 0.0	0		
Paraeuchaeta norvegica C6	0.0 ± 0.0	0.1	0.0 ± 0.0	0	0.0 ± 0.0	0.1			0.1 ± 0.1	0.6	0.0 ± 0.0	0	0.0 ± 0.1	0.5		
Paraeuchaeta spp. C1–C5	0.4 ± 0.2	0.7	0.4 ± 0.3	6.0	0.1 ± 0.1	0.3	0.0 ± 0.0	0	0.6 ± 0.8	3.2	0.6 ± 0.5	1.8	0.6 ± 0.9	3.8	0.2 ± 0.5	1.7
Paraheterorhabdus compactus C4–C6									0.0 ± 0.0	0						
Pleuromamma robusta C6F	0.0 ± 0.0	0.1	0.0 ± 0.0	0					0.0 ± 0.1	0.4	0.0 ± 0.0	0	0.0 ± 0.1	0.4		
Pseudocalanus acuspes C6F	2.1 ± 2.5	4.8	1.4 ± 2.0	S	11.4 ± 13.1	48.6	55.7 ± 54.0	135.7	0.1 ± 0.1	0.3	1.5 ± 1.6	5.7	3.4 ± 2.7	10.5	$\begin{array}{c} 10.0 \pm \\ 12.8 \end{array}$	47.8
Pseudocalanus minutus C6F	0.5 ± 0.7	1.6	0.8 ± 1.2	2.7	3.0 ± 2.7	12.1	10.1 ± 10.6	29.8	0.8 ± 0.6	2.4	3.3 ± 3.8	16.7	3.4 ± 2.8	10.4	7.1 ± 9.3	33.3
Pseudocalanus spp. C1–C5, C6M	6.7 ± 4.3	12.1	64.9 ± 109.2	259.2	165.9 ± 91.8	396	1119.1 ± 915.6	2314.4	7.3 ± 5.7	18.6	94.1 ± 92.4	342.7	177.3 ± 120.6	683.8	302.4 ± 220.5	855.1
Pseudochirella spectabilis C4–C6									0.0 ± 0.0	0						
Rhincalanus nasutus C4–C6									0.0 ± 0.0	0.1	0.0 ± 0.1	0.4				
Scaphocalanus brevicornis									0.1 ± 0.1	0.4						

Scaphocalanus magnus									0.0 ± 0.0	0.1						
Scolecithricella minor	0.3 ± 0.2	0.6	0.2 ± 0.2	0.4	0.1 ± 0.1	0.6			0.4 ± 0.4	1.4	0.4 ± 0.3	1.1	0.3 ± 0.4	1.9	0.2 ± 0.5 1	1.7
Spinocalanus antarcticus									0.0 ± 0.1	0.2						
Spinocalanus horridus C4–C6									0.1 ± 0.1	0.4						
Spinocalanus longicornis C6									0.0 ± 0.1	0.2						
Spinocalanus spp. C1–C6					0.0 ± 0.0	0			0.1 ± 0.1	0.4						
Temorites brevis									0.0 ± 0.0	0						
Tharybidae indet. C4-C6									0.1 ± 0.1	0.4						
Tharybis groenlandicus C6									0.0 ± 0.0	0						
Triconia borealis C6					6.5 ± 12.8	62.6	3.6 ± 9.5	25.2	20.4 ± 12.0	44.3	23.4 ± 18.4	76.7	23.2 ± 37.4	216.4	$\begin{array}{c c}11.1 \pm \\15.7\end{array}$	59.1
Triconia conifera C6F	0.0 ± 0.0	0							0.0 ± 0.0	0.1			0.0 ± 0.1	0.8		
Triconia/Oncaea spp. C1-C5	0.0 ± 0.0	0	0.1 ± 0.2	0.5	0.1 ± 0.2	1	0.2 ± 0.6	1.6	0.1 ± 0.4	1.5	0.2 ± 0.4	1.1	0.1 ± 0.3	1.6	0.1 ± 0.3 1	1.1
Undinella oblonga C4–C6									0.0 ± 0.0	0						
Xantharus siedleckii					0.0 ± 0.1	0.4							0.0 ± 0.0	0.2		
	;		:	,	•	0	•									

Missing values indicate zero occurrences, while values marked 0.0 mean <0.04 ind. m^{-3}

Table 7.6 Total abundance (ind. m⁻³) of other taxa than copepods in different areas of Kongsfjorden during the periods 1994–2006 and 2007–2016, based on Multinet samples

•																
	1999–2006								2007-2016							
	Fram Strait		Shelf		Outer basir	5	Inner basin		Fram Strait		Shelf		Outer basin		Inner basin	
	Mean ±		Mean ±		Mean ±		Mean ±		Mean ±		Mean ±		Mean ±		Mean ±	
Таха	StDev	Мах	StDev	Мах	StDev	Max										
Amphipoda																
Amphipoda indet.			0.0 ± 0.0	0	0.0 ± 0.0	0	0.0 ± 0.0	0.1	0.0 ± 0.1	0.3			0.0 ± 0.1	0.4	0.0 ± 0.0	0.1
Apherusa glacialis									0.0 ± 0.0	0			0.0 ± 0.1	0.4		
Cyclocaris guilelmi									0.0 ± 0.0	0						
Eusirus holmii									0.0 ± 0.1	0.4						
Hyperia galba			0.0 ± 0.0	0	0.0 ± 0.0	0	0.0 ± 0.0	0								
Hyperiidae indet.	0.0 ± 0.0	0														
Hyperoche medusarum					0.0 ± 0.0	0							0.0 ± 0.0	0		
Onisinus spp.					0.0 ± 0.0	0										
Scina borealis									0.0 ± 0.1	0.4						
Themisto abyssorum	0.5 ± 0.2	0.7	0.4 ± 0.2	0.7	0.7 ± 0.7	4	1.0 ± 1.1	2.7	0.4 ± 0.5	2.1	0.9 ± 0.6	2.3	1.2 ± 0.7	2.6	1.7 ± 2.3	<i>T.</i> 7
Themisto libellula	0.0 ± 0.0	0.1	0.0 ± 0.0	0.1	0.5 ± 0.8	3.9	3.0 ± 4.2	9.4	0.0 ± 0.0	0.1	0.2 ± 0.3	1.1	0.3 ± 0.4	1.6	0.5 ± 0.6	1.6
Euphausiacea																
Euphausiacea indet. (larvae)	0.1 ± 0.1	0.2	0.2 ± 0.1	0.3	0.0 ± 0.1	0.4	0.2 ± 0.3	0.6	0.9 ± 1.2	4.7	0.8 ± 0.8	2.3	0.4 ± 0.6	2.5	0.4 ± 0.4	1.2
Meganycti-phanes norvegica	0.0 ± 0.0	0			0.0 ± 0.0	0	0.0 ± 0.0	0.1	0.0 ± 0.0	0	0.0 ± 0.0	0				
Thysanoessa inermis	0.1 ± 0.1	0.3	0.0 ± 0.0	0.1	0.0 ± 0.0	0.1	0.2 ± 0.2	0.4	0.0 ± 0.0	0	0.0 ± 0.0	0	0.1 ± 0.2	0.8	1.1 ± 1.0	4

ntinued)	(co															
1659.5	194.9 ± 416.1	1887.6	195.5 ± 360.3	89.6	28.1 ± 30.7	15.6	2.6 ± 5.2	4188.9	966.9 ± 1473.6	564.9	57.6 ± 127.7	12.5	5.4 ± 5.6	9.2	3.7 ± 4.2	Bivalvia larvae and juveniles
																Meroplankton
										0	0.0 ± 0.0					Tanaidacea indet.
		0	0.0 ± 0.0							0	0.0 ± 0.0					Pseudomma truncatum
1.4	0.2 ± 0.4	1.5	0.2 ± 0.4	1.8	0.4 ± 0.5	4.5	1.8 ± 1.0	19.1	2.8 ± 7.2	0.9	0.2 ± 0.2	1.1	0.6 ± 0.4	1.3	1.0 ± 0.3	Ostracoda indet.
										0	0.0 ± 0.0					Mysidae indet.
1.5	0.1 ± 0.4	1.3	0.1 ± 0.2	0.2	0.0 ± 0.1	0.4	0.0 ± 0.1	0.4	0.1 ± 0.1	1.1	0.2 ± 0.2	0.1	0.1 ± 0.0	0.1	0.0 ± 0.0	Isopoda indet.
						0	0.0 ± 0.0							0	0.0 ± 0.0	Hymenodora glacialis
1.2	0.2 ± 0.4	3.7	0.7 ± 1.0	1.2	0.2 ± 0.4	0	0.0 ± 0.0			1.9	0.2 ± 0.4			0	0.0 ± 0.0	Facetotecta indet.
				104.7	5.5 ± 24.0							24.2	4.9 ± 10.8	4.7	1.2 ± 2.3	Evadne nordmanni
		0	0.0 ± 0.0	0	0.0 ± 0.0											Eusergestes arcticus
		0.4	0.0 ± 0.1							0.2	0.0 ± 0.0					Cumacea indet.
		0.1	0.0 ± 0.0							0	0.0 ± 0.0					Boreomysis arctica
4.6	1.1 ± 1.2	2.3	0.6 ± 0.6	0.8	0.3 ± 0.3	1	0.1 ± 0.3	1.9	0.3 ± 0.7	0.2	0.0 ± 0.1					Bopyridae indet.
																Other Crustacea
2.4	0.3 ± 0.6	0.5	0.0 ± 0.1	23.2	1.2 ± 5.3			0.4	0.1 ± 0.2	0.2	0.0 ± 0.0	5.7	1.1 ± 2.5	0	0.0 ± 0.0	Thysanoessa raschii
0.5	0.1 ± 0.2	0.1	0.0 ± 0.0	0.2	0.0 ± 0.1	0.8	0.1 ± 0.2	0.9	0.2 ± 0.3	0.1	0.0 ± 0.0	0.6	0.2 ± 0.3	0.6	0.3 ± 0.3	Thysanoessa longicaudata

 Table 7.6 (continued)

	1999–2006								2007–2016							
	Fram Strait		Shelf		Outer basin	_	Inner basin		Fram Strait		Shelf		Outer basin		Inner basin	
E	Mean ±	;	Mean ±	;	Mean ±	;	Mean ±	:	Mean ±		Mean ±	;	Mean ±	;	Mean ±	
Taxa	StDev	Max	StDev	Max	StDev	Max	StDev	Max	StDev	Max	StDev	Max	StDev	Max	StDev	Max
Bryozoa larvae	0.0 ± 0.0	0	0.0 ± 0.0	0	0.1 ± 0.2	0.8	0.4 ± 0.6	1.6	0.0 ± 0.0	0.1	0.0 ± 0.0	0.1	0.1 ± 0.3	1.2	0.1 ± 0.5	2.3
Cirripedia nauplii and cyprid	0.0 ± 0.0	0.1	0.1 ± 0.1	0.2	0.7 ± 0.9	3.3	7.7 ± 10.0	22.9	0.0 ± 0.1	0.3	0.5 ± 0.9	4.1	4.3 ± 14.4	81.5	2.2 ± 3.3	13.1
Decapoda larvae	0.0 ± 0.0	0.1	0.0 ± 0.1	0.2	0.0 ± 0.0	0.1	0.7 ± 1.1	2.7					0.0 ± 0.0	0.1	0.0 ± 0.1	0.5
Echinodermata larvae	2.6 ± 0.7	3.3	21.5 ± 14.4	39.7	111.5 ± 261.9	1211.3	261.7 ± 449.1	1244.8	0.4 ± 0.5	1.5	36.4 ± 54.0	189.4	59.5 ± 58.2	248.6	30.0 ± 55.0	165.6
Gastropoda larvae			0.0 ± 0.0	0.1	0.1 ± 0.2	0.9			0.0 ± 0.1	0.2	0.3 ± 0.5	1.3	5.6 ± 31.4	199.4	0.8 ± 1.9	7.6
Hyas araneus			0.0 ± 0.0	0	0.0 ± 0.1	0.4			0.0 ± 0.0	0	0.0 ± 0.0	0.1	0.1 ± 0.2	1		
Nemertea pilidium					0.0 ± 0.1	0.4	0.1 ± 0.2	0.5			0.0 ± 0.0	0.1	0.0 ± 0.1	0.3	0.0 ± 0.0	0.2
Pagurus pubescens	0.0 ± 0.0	0			0.0 ± 0.0	0	0.2 ± 0.4	0.0			0.0 ± 0.2	0.8	0.0 ± 0.1	0.7	0.2 ± 0.4	1.5
Pandalus borealis					0.0 ± 0.0	0	0.0 ± 0.0	0.1			0.0 ± 0.0	0.1	0.0 ± 0.1	0.7	0.1 ± 0.2	0.5
Polychaeta larvae	0.1 ± 0.1	0.3	0.4 ± 0.4	1	3.5 ± 5.8	27.3	13.5 ± 16.4	42.1	0.3 ± 0.3	1	1.2 ± 0.9	3.5	2.9 ± 1.7	7.1	1.9 ± 3.7	15.3
Sabinea septemcarinata					0.0 ± 0.1	0.6									0.0 ± 0.1	0.5
Typhloscolecidae larvae									0.1 ± 0.2	0.8	0.0 ± 0.0	0	0.0 ± 0.0	0.1		
Cnidaria																
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Aeginopsis laurentii					0.0 ± 0.0	0					0.0 ± 0.1	0.2				
Aglantha digitale	2.2 ± 2.8	6.1	0.5 ± 0.8	1.9	0.2 ± 0.3		0.1 ± 0.2	0.5	0.4 ± 0.7	2.4	1.1 ± 2.5	10.7	0.3 ± 0.6	2.4	0.1 ± 0.3	1
Botrynema ellinorae									0.1 ± 0.2	0.8	0.0 ± 0.1	0.2				
Bougainvillia spp.													0.0 ± 0.0	0.1		
Dimophyes arctica	0.1 ± 0.1	0.2	0.0 ± 0.0	0.1	0.0 ± 0.0	0.1			0.1 ± 0.2	0.8	0.0 ± 0.0	0.2	0.0 ± 0.0	0		
Halitholus cirratus	0.0 ± 0.0	0			0.0 ± 0.0	0			0.0 ± 0.0	0			0.0 ± 0.0	0.1		
Hydrozoa indet.			0.0 ± 0.0	0.1	0.0 ± 0.0	0.1			0.0 ± 0.0	0	0.0 ± 0.2	0.8	0.1 ± 0.2	0.8	0.0 ± 0.2	0.7
Nanomia cara									0.0 ± 0.0	0						
Sarsia sp.			0.1 ± 0.1	0.2	0.0 ± 0.0	0										
Scyphozoa indet.													0.0 ± 0.0	0.2		
Siphonophora indet.					0.0 ± 0.0	0			0.0 ± 0.0	0			0.0 ± 0.0	0		
Ctenophora																
Beroë cucumis	0.0 ± 0.0	0	0.1 ± 0.1	0.1	0.2 ± 0.3	1.5	0.9 ± 2.3	6.1	0.0 ± 0.0	0.1	0.1 ± 0.1	0.5	0.1 ± 0.2	1	0.0 ± 0.1	0.2
Ctenophora									0.0 ± 0.0	0.1	0.0 ± 0.1	0.6	0.0 ± 0.0	0.1		
Mertensia ovum			0.7 ± 1.2	2.8	0.1 ± 0.2	0.7	0.1 ± 0.2	0.7	0.0 ± 0.1	0.4	0.3 ± 1.0	4.3	0.1 ± 0.2	0.6	0.2 ± 0.4	1.5
Pteropoda																
Clione limacina	0.0 ± 0.0	0	44.7 ± 81.5	187.8	0.4 ± 1.7	10.6	0.3 ± 0.5	1.5	0.1 ± 0.2	0.8	1.9 ± 7.9	34.6	0.1 ± 0.2	0.7	0.1 ± 0.2	0.7
															(con	tinued)

(continued)	
7.6	
Table	

	1999–2006	,c							2007-2016							
	Fram Strai	t.	Shelf		Outer basin	_	Inner basin		Fram Strait		Shelf		Outer basin		Inner basin	
	Mean ±		Mean ±		Mean ±		Mean ±		Mean ±		Mean ±		Mean ±		Mean ±	
Taxa	StDev	Max	StDev	Мах	StDev	Max	StDev	Max	StDev	Max	StDev	Мах	StDev	Max	StDev	Max
Limacina helicina	0.3 ± 0.6	1.1	8.2 ± 12.2	27.3	2.8 ± 5.6	23.1	4.2 ± 7.3	16.9	0.3 ± 0.4	1.2	45.6 ± 148.7	647.2	65.7 ± 195.5	968.5	178.6 ± 543.2	2277.5
Limacina retroversa	0.1 ± 0.2	0.4	0.2 ± 0.3	0.6	0.0 ± 0.1	0.4	0.1 ± 0.2	0.5	0.0 ± 0.1	0.2	0.1 ± 0.3	1	0.1 ± 0.5	2.6		
Annelida																
Pelagobia sp.	0.1 ± 0.1	0.3							0.1 ± 0.2	0.8	0.0 ± 0.1	0.5	0.0 ± 0.0	0.1		
<i>Tomopteris</i> <i>helgolandica</i>									0.0 ± 0.0	0.1						
Tomopteris spp.	0.0 ± 0.0	0.1			0.0 ± 0.0	0.2										
Chaetognatha																
Eukrohnia hamata	3.2 ± 1.5	5.3	5.6 ± 2.2	9.1	1.7 ± 1.3	5	0.1 ± 0.2	0.5	3.6 ± 2.3	9.2	3.7 ± 2.7	11.3	2.4 ± 3.0	15.5	0.7 ± 1.6	6.5
Parasagitta elegans	0.2 ± 0.1	0.4	0.9 ± 1.2	2.9	2.4 ± 1.5	6.6	13.2 ± 13.4	41.4	0.1 ± 0.1	0.3	0.8 ± 0.8	2.4	2.2 ± 1.5	٢	4.8 ± 3.5	11.8
Pseudosagitta maxima									0.0 ± 0.0	0						
Cephalopoda																
Cephalopoda											0.0 ± 0.0	0	0.0 ± 0.0	0		
Appendicularia																
Appendicularia													0.0 ± 0.0	0.1		
Fritillaria borealis	0.7 ± 1.0	2.1	13.9 ± 19.7	44.1	31.7 ± 51.4	250.3	22.4 ± 50.4	136.1	4.3 ± 10.0	37.8	21.8 ± 32.1	9.06	10.3 ± 14.0	53	3.8 ± 8.7	36.2
Oikopleura spp.	1.7 ± 2.6	5.5	7.8 ± 9.6	21.5	2.8 ± 2.9	10.7	0.0 ± 0.0	0.1	0.6 ± 0.7	2.2	17.5 ± 31.9	131.4	5.0 ± 5.5	23.4	2.1 ± 7.0	29.8
Pisces					0.0 ± 0.0	0	0.0 ± 0.0	0.1	0.0 ± 0.0	0			0.0 ± 0.0	0.1		
Missing wolung indi	0000 2000 0	0.000	lidm occar	infort o	polyon or	0.0 0.0	pui 10 07 u									

Missing values indicate zero occurrences, while values marked 0.0 mean <0.04 ind. m⁻³



Fig. 7.7 Changes in biomass of most commonly encountered krill and amphipod species in the zooplankton time series sampled from 1996–2016 by MultiNet (200 μ m mesh size). See Fig. 7.6 for explanation

of other copepod species were less clear (Fig. 7.6). As an example, the biomass of the Arctic *T. borealis* appears to have increased: the species appeared irregularly in the samples until 2009 and occurred in low biomass thereafter.

7.4.2 Amphipods and Euphausiids

The biomass of larger crustaceans, such as *T. libelulla*, *T. abyssorum* and euphausiids, also followed similar temporal patterns as found for *Calanus* spp. and small copepods inside the fjord (Fig. 7.7). However, the increase in biomass started already in 2006 and was most pronounced after 2010 for the Atlantic *T. abyssorum* in the outer basin. The Arctic *T. libellula* showed a peak in biomass around 2000–2001, particularly in the inner basin. After a decline in mid-2000, it increased in biomass from 2008, but then decreased in the inner basin after 2009. On the shelf and in Fram Strait, there was no distinct temporal trend for these larger crustaceans. Krill, particularly *T. inermis* and to a lesser extent *T. longicaudata*, increased in abundance during the warming period in 2006–2007, mainly in the inner basin (Fig. 7.7). While abundance estimates from MultiNet may underestimate their true abundance, the data should nevertheless be comparable within the time series since the method remained the same throughout the time series. Thus, changes in their occurrence in the samples should reflect changes in the environment between years, i.e. years/locations with high abundance should result in higher numbers caught in the MultiNet compared to years/locations with low abundance.

Seasonal abundance (ind. m^{-3}) for euphausiids and pelagic amphipods, based on composite data from the outer basin from April to October (Fig. 7.8), also include abundance estimate from larger nets that catch these groups more efficiently (see Methods). Highest abundances of the *T. inermis*, *T. longicaudata* and *T. raschii* have been recorded during spring, while they declined through the summer. *Meganyctiphanes norvegica* was mainly caught in October, but was also present during spring-summer, with juveniles in April. The pelagic amphipods *T. libellula* and *T. abyssorum* had highest abundances during July, and the abundance of *T. abyssorum* remained elevated though the autumn.

7.4.3 Changes in Zooplankton Abundance 1996–2006 Versus 2007–2016

The time-series patters were best visualized by patterns in biomass (Figs. 7.6 and 7.7), whereas the seasonal data for krill and amphipods were based on abundance (Fig. 7.8). The abundance of copepods (Table 7.3) and other taxa (Table 7.4), including their spatial distribution in Kongsfjorden (Tables 7.5 and 7.6) have shown changes in abundance from the early (1996-2006) to the later sampling period (2007–2016). The abundance of C. finmarchicus more than doubled in Kongsfjorden from a mean of 176 to 431 ind. m⁻³, and maximum values increased by a factor of six between the two periods (Table 7.3). At the same time, the abundance of C. glacialis remained about the same, 90-100 ind. m⁻³. The abundance of Pseudocalanus sp. decreased to about half after 2006. Small copepods, such as O. similis were also reduced by about 25% during the later period. Changes related to abundance of other taxa included an increase in the pteropod L. helicina from 5 to 72 ind. m^{-3} . Particularly the maximum increased substantially, from 86 to 2278 ind. m⁻³ between periods, reflecting the ephemeral mass occurrence of this species during summer. Changes in larger zooplankton generally reflected changes in biomass, as described above.



Fig. 7.8 Seasonal variability in mean abundance (ind. m^{-3}) of euphausiids (*Thysanoessa inermis*, *T. longicaudata, Meganyctiphanes norvegica*, and *T. raschii*) and pelagic amphipods (*Themisto libellula* and *T. abyssorum*) for the outer basin of Kongsfjorden. Data are combined for stations and sources, with samples from MultiNet as well as MIK and Tucker trawl (Dalpadado et al. 2016; Long-term series, F. Buchholz unpubl.). Number of replicates (stations and samplings) for each month is given in parenthesis under x-axis labels. Error bars that reach all the way down to zero represent negative minimum CIs indicating low confidence for the mean estimate. The figure contains data from 2006–2013

7.4.4 Effect of Temperature on the Zooplankton Community

The zooplankton community within Kongsfjorden appears to have responded differently to environmental changes compared to the communities outside Kongsfjorden (Fig. 7.9). While Atlantic species (*C. finmarchicus, O. atlantica, T. abyssorum, T. longicaudata*) have generally increased in abundance and biomass in inner Kongsfjorden (Fig. 7.9), the opposite pattern appears to have happened outside Kongsfjorden with an increase in some Arctic species (*T. libellula* and *C. hyperboreus*).

Water depth, type and temperature as well as year and station location fitted best to the unconstrained PCA ordination using the zooplankton abundance community matrix (Table 7.7). Due to interactions caused by station location along the timeseries transect, the dataset was split into two community matrices: samples from the inner and outer basin, and samples from the shelf and Fram Strait stations. The resulting ordinations were further constrained to the best fitting linear gradients: depth, year and temperature. The fit of station location and region to the resulting RDA ordinations were rather low indicating that these factors explained the split datasets poorly (Table 7.7). Temperature and contribution of Atlantic Water increased throughout the study period (Fig. 7.2), but temperature and sampling depth were negatively correlated making it difficult to separate the effects of these variables on the zooplankton community composition. Nevertheless, temperature and depth "explained" well the community ordination with R² values between 0.41 and 0.55 (Table 7.7). Metridia longa and Microcalanus spp. were generally more abundant in deep or cold habitats than O. similis, Echinodermata, Bivalvia, copepod nauplii and C. finmarchicus (Fig. 7.10). Also O. atlantica was identified by the RDA to have increased in recent years, but the increase may have been caused by exceptional high biomass in 2014, while there was no clear increasing trend in the biomass of this species over the entire time period. Microcalanus spp., on the other hand, showed a trend towards an increase outside Kongsfjorden. Salinity explained poorly the average community composition (Table 7.7).

Fig. 7.9 (continued) 95% confidence intervals. If the error bars do not cross the zero-line, the difference in biomass between warm and cold years is statistically significant. Significant LnR values have been indicated with red for higher values during warm years and with blue for higher values during cold years. Values on the y-axis are natural logarithms of mean biomass ratio for a given region and the range for y-axes vary among taxa. Colours for taxa names indicate the origin relative to the study location: red implies Atlantic, blue Arctic origin, and black indicates species that originates from both regions. Averaged biomasses over all depth-strata within a MultiNet multiple plankton sampler (MPS) cast were used as replicates and the ranges of number of replicates are given under a taxa name for warm years/cold years. Size of mean LnR point is scaled with the minimum number of replicates available for each Region



Fig. 7.9 Logarithmic response ratio (LnR) analysis of zooplankton taxa biomass allocation between warm and cold years. Values >0 indicate that biomass of given taxa was higher during the warm years compared to the cold years, and values <0 indicate the opposite. Error bars indicate

7.5 Discussion of Data from the 20-Year Time Series in Context with Other Data

The mesozooplankton community in Kongsfjorden resembles, in many aspects, communities found in pelagic ecosystem in other Svalbard fjords and the northern Barents Sea, with a dominance of copepods in terms of species numbers, a numerical dominance of small-sized copepods and biomass dominance of larger copepods of the genus *Calanus*.

7.5.1 Interannual and Long-Term Changes

Recent decades have revealed large changes in the West Spitsbergen Current and a general warming of the Arctic (Beszczynska-Möller et al. 2012: Walczowski et al. 2012). The long observation record (2000–2017) from Fram Strait showed the warming peak around 2006, but has not revealed a general warming for the water column (Walczowski et al. 2017). However, the salinity has increased during this period as did the temperature in the Atlantic water layer in Fram Strait, which likely has affected the heat transport to West Spitsbergen and the Arctic Ocean. Given the seascape of Kongsfjorden and its neighbourhood, oceanographic conditions outside the fjord do affect the advection of water masses into it and, thus, the hydrological conditions inside the fjord. Particularly, two warming anomalies of Atlantic Water passing through Fram Strait in 1999–2000 and 2005–2007 have been responsible for two major warming periods in Kongsfjorden in 2001 and 2006 (Fig. 7.2; Tverberg et al., Chap. 3). In addition, climate warming affects ice conditions, glacier run-off and water temperatures directly in the fjord (Sundfjord et al. 2017). Atlantic or Transformed Atlantic Water occupy Kongsfjorden to a variable degree, and can modify the zooplankton community accordingly (Ormanczyk et al. 2017; Prominska et al. 2017; Weslawski et al. 2017). Previous studies from Kongsfjorden have related the proportions of zooplankton species with different biogeographic origins to the distribution of Arctic and Atlantic water masses and their mixing and exchange on the shelf (Kwasniewski et al. 2003; Basedow et al. 2004; Cottier et al. 2005; Willis

Fig. 7.10 (continued) the Shelf and Fram Strait stations. Individual samples from a MPS (MultiNet multiple plankton sampler) cast were used as "sites" and are illustrated using grey dots. Species scores are illustrated using red crosses and species abbreviations for scores with absolute value >0.4 are presented as labels where the line points to the corresponding cross. Species names are abbreviated from Table 7.2. Twelve most contributing species to RDA axes 1 and 2 have been shown in "lollipop charts" on the right side of RDA plots. The y-axis value responds to the axis score, and values inside the heads indicate the contribution of a given species to total axis eigenvalue with all species in the dataset adding up to 100%. Heads are color-coded with red indicating shallower sampling depths, warmer temperatures or/and later years during the time series than the blue heads, which are the opposite. Total PCA inertia explained by each RDA axis is given in parenthesis in axis labels



Fig. 7.10 Redundancy analysis (RDA) of the zooplankton abundance time series (1996–2016) with temperature, maximum depth of sampling strata and year as linear environmental gradients (green arrows). (a) The analysis for Inner and Outer basins of Kongsfjorden, and (b) analysis for

	All		Inner and	d outer basins	Shelf an	d Fram strait
Variable	R ² _{factor}	R ² _{vector}	R ² factor	R ² _{vector}	R ² _{factor}	R ² _{vector}
Depth	0.41	0.34	0.46	0.55	0.45	0.40
Temperature		0.43		0.48		0.40
Year	0.17	0.02	0.43	0.47	0.34	0.52
Water mass	0.27		0.27		0.18	
Station	0.25		0.03		0.14	
Region	0.23		0.01		0.10	
Salinity		0.11		0.12		0.05
Warm vs. cold year	0.06		0.11		0.01	

Table 7.7 Explanatory variable fit to the unconstrained PCA ordination (Region = All) and to the constrained RDA ordinations (Region = Inner and Outer basins, and Shelf and Fram Strait) using the zooplankton abundance community matrix

 R^2_{Factor} gives the coefficient of determination for variables that were treated as categorical leading to centroid fits and allowing nonlinearity, while R^2_{Vector} gives similar value for continuous variables treated as linear gradients

et al. 2006, 2008; Buchholz et al. 2010; Dalpadado et al. 2016; Gluchowska et al. 2016). Thus, variable and increased inflow of Atlantic Water, with warming trend inside the fjord during our observation period (Fig. 7.2) and resulting changes in the pelagic fauna phenology, may be responsible for the observed changes in the zoo-plankton community of the fjord between 1996 and 2002 (Hop et al. 2006) and 2006–2016.

However, only few species showed clear trends of either increase or decrease in the time series. Large interannual variations in C. finmarchicus abundance and biomass seem to be correlated to changes in hydrography, particularly the influx of Atlantic Water, i.e. warm years led to an increased abundance of C. finmarchicus compared to cold years. Calanus finmarchicus is an Atlantic boreal deep-water species and considered an expatriate species in the Arctic. The ability of C. finmarchicus to survive and colonize the Arctic Ocean is hampered by short algal blooms and low temperatures (Jaschnov 1970; Tande and Båmstedt 1985; Ji et al. 2012), and it fails to reproduce in the Arctic Ocean and partly also in the surrounding shelf seas (Hirche et al. 2006). The high interannual variability in C. finmarchicus abundance in Kongsfjorden may indicate that the species in Kongsfjorden is composed of a resident population reproducing locally and an advected one reproducing outside the fjord, most likely in the WSC. Thus, the abundance in the fjord is dependent on the strength of the inflow from the outside, with strong inflow of Atlantic Water and consequently an increased abundance of that species in what is referred to as "warm years" (Espinasse et al. 2017). In such years, the size of the population in the WSC also increases (Gluchowska et al. 2017; Weydmann et al. 2018). Furthermore, the variability in C. finmarchicus abundance in Kongsfjorden may not only be explained by variability in advection, but also by variability in local reproduction, which is more successful during "warm years" leading to increased population size (Kwasniewski et al. 2013).

Calanus glacialis, on the other hand, is an Arctic shelf species, spawning in waters all around the Arctic shelf and in the White Sea (Kosobokova 1999; Daase et al. 2013). This species displays high flexibility in its reproductive strategies as an adaptation to living in seasonal ice covered seas with high inter-annual variability in the timing of ice break up and bloom phenology. Relatively little variability in C. glacialis abundance in Kongsfjorden indicates that Kongsfjorden harbours a resident C. glacialis population that is successfully reproducing there (Kwasniewski et al. 2003), but can also include a supplementary population from outside the fjord, advected with the coastal current. The results of our observations showed no clear impact of changes in environmental factors on the number or biomass of C. glacialis. The inter-annual variability observed in its biomass is likely related to the stage composition at the time of sampling, as biomass increases with developmental stage; adult specimens might have six times as much biomass as a young copepodids (copepodid stages C1-C3). Thus, low biomass may indicate higher abundance of small stages and not a general decrease in abundance. For example, the C. glacialis population in 2010 consisted to >70% of copepodid stages C1-C3 leading to low biomass in the inner basin, while in 2013 (high biomass) the population consisted >80% of C4 and C5. These differences in stage composition between years reflect differences in phenology (for this species as well as others), including timing of reproduction, which is tightly coupled to the onset, duration and magnitude of the spring bloom, which can vary considerable between years (Daase et al. 2013; Hegseth et al., Chap. 6). The spring bloom occurred earlier (mid-May) in 2013 than in some of the previous years (mid-June in 2010 and 2011), which may explain the high percentage of older copepodids in 2013. The persistence of Arctic C. glacialis in the zooplankton community demonstrates that this species can tolerate a wide range of environmental conditions and suggests that ongoing changes in the environmental conditions in Kongsfjorden have not reached critical levels for this species.

Temporal trends were apparent in larger crustaceans, with increased biomasses of the Atlantic amphipod T. abyssorum and euphausiids (T. inermis, T. longicaudata) in the most recent years and decreased abundance of the Arctic Themisto libellula. Increase in T. abyssorum has also been recorded in the HAUSGARTEN area of Fram Strait and related to the prevailing influence of North Atlantic water masses in the upper part of the water column (Kraft et al. 2012). We recognize that larger individuals of these species may be undersampled by MultiNet, and high predatory mortality by e.g. capelin (Mallotus villosus) may impact krill densities in Kongsfjorden (Dalpadado et al. 2016). Population increases in the currently present five species of krill were noted with the exception of T. raschii, and the seasonal data (with samples from larger nets) indicate that they are most abundant in the fjord during spring. Overall, the Arcto-boreal expatriate T. inermis appears to be well suited to withstand the challenges of an Arctic environment with vital rates similar to temperate species and congeners (Huenerlage and Buchholz 2015). The vital rates typically remain high during the spring bloom, but then drop during the summer. Changes in krill occurrence may indicate changes in food-webs; if krill numbers increase around Svalbard - i.e. on the basis of the successful completion of a full reproductive cycle for *Thysanoessa* spp., higher trophic levels will likely follow them. In the Barents Sea, increasing krill numbers during the last decades may have supported substantial increases in fish stocks (Eriksen and Dalpadado 2011). The rapid increase in population density in Kongsfjorden may be interpreted as consequence of increasing Atlantic input, which carried the krill along having been spawned in the warming Barents Sea. However, a proportional change in the repertoire of krill species in the Arctic and sub-Arctic waters would possibly lead to a decrease in the availability of the lipid-rich, high-quality food represented by *T. inermis* that would likely be replaced by the currently strongest expanding krill species *M. norvegica*, which carries far less lipids, (Huenerlage et al. 2016). This Atlantic species was present in the outer basin of Kongsfjorden mainly during the late autumn, but is more abundant outside Kongsfjorden (Dalpadado et al. 2016).

7.5.2 Potential Effects of Changes in Winter Temperatures

Temperature time series from ocean observatories have shown that the largest temperature increase in the fjord over the last decade occurred during winter (Geoffroy et al. 2018; Hop et al., Chap. 13). This is in agreement with results of studies on water-mass transport in the West Spitsbergen Current, which show that that in winter the WSC tends to be wider and stronger with two-fold higher transport (Beszczynska-Möller et al. 2012). Zooplankton abundance and species composition recorded during surveys may to some degree reflect the occurrence of water masses just prior to or during sampling, particular in open water and highly advective regions. However, hydrographic events and progress occurring in previous seasons may also have an effect on how zooplankton communities are structured during summer, particular in more secluded locations such as fjords. Increased winter temperatures may affect the survival of zooplankton populations either negatively (due to increased metabolic cost at increased water temperature) or positively (more favourable conditions for boreal species advected during summer and autumn that may otherwise not survive under cold Arctic winter conditions). Furthermore, zooplankton advected with inflowing Atlantic Water during winter (e.g. Cottier et al. 2007) may persist throughout the year. Thus, some of the long-term changes discussed above may be related to the increase in winter temperatures in Kongsfjorden. For example, the higher biomass of C. finmarchicus in recent years may be due to increased winter survival related to more favourable (i.e. higher) winter temperatures, which may also have caused favourable bloom phenology (see below) increasing recruitment in the local population during spring. However, we generally lack long-term seasonal data on zooplankton from Kongsfjorden, except for a few studies (Walkusz et al. 2009; Lischka and Hagen 2016), and therefore cannot determine seasonally-delayed effects on the zooplankton composition during summer. Furthermore, more factors than just winter temperature need to be considered, such as the effect of increased winter temperatures on duration of sea ice cover and timing of spring plankton blooms, in addition to the timing of advection. Future monitoring efforts may benefit from increased seasonal sampling resolution to untangle these effects.

7.5.3 Sea Ice, Plankton Blooms and Increased Bio-production in Ice-Free Waters

Arctic zooplankton communities are also affected by sea ice. Sea ice limits the penetration of light into the water column and the freeze/melt cycle of sea ice affects water mass stratification and mixing processes. These physical processes control the replenishment of essential nutrients to the euphotic zone, and thereby the onset and duration of ice algae and pelagic blooms (Søreide et al. 2010; Leu et al. 2015). The timing, quality and quantity of these blooms influence recruitment, growth and development of primarily herbivorous zooplankton species (Leu et al. 2011). One of the major changes between the 1996–2006 and the 2007–2016 period is the loss of sea ice in Kongsfjorden. The fjord had little ice cover of only short duration after 2006, except for 2009 and 2011 when the ice coverage was more extensive but thinner than in earlier years (Pavlova et al., Chap. 4). Several controlling factors, such as winter/early spring convections and mixing, in addition to duration of sea ice cover, are involved in the timing of the spring bloom in Kongsfjorden, which varies from mid-late April to late May or early June (Hegseth et al., Chap. 6).

The general increase in zooplankton abundance between these two periods likely reflects these changes: the loss of sea ice was accompanied with increased (winter) temperatures promoting growth and development, and the peak of the bloom typically happens 2–3 weeks after the ice break-up (Hegseth et al., Chap. 6). However, the magnitude of the bloom is also dependent on stratification of water masses, which is weaker in cold years than in warm years in Kongsfjorden. The algae species composition also changes with dominance of diatoms in cold years and more flagellates and prolonged blooms throughout the summer months during warm years (Hegseth et al., Chap. 6). Thus, for C. glacialis the conditions become more favourable during the cold years with early spring blooms of diatoms, whereas for C. finmarchicus, Atlantic amphipods and krill the conditions get better during warm years. Espinasse et al. (2017) related years with higher C. finmarchicus abundance in Kongsfjorden to years with a delayed spring bloom, which they explained with improved feeding conditions for the younger developmental stages accelerating growth and development of the boreal calanoid. The decrease in sea ice during the last decades in the European Arctic, including Svalbard waters, has opened up large areas for new bio-production (Smedsrud et al. 2013; Falk-Petersen et al. 2015). This has led to higher production of herbivorous zooplankton as well as higher trophiclevel animals (Eriksen et al. 2017). A similar pattern can be seen for Kongsfjorden with regard to total biomass of zooplankton (Fig. 7.11). The biomass has generally increased in Kongsfjorden during the last decade, which infers a probable increase in bio-production, although this pattern was less apparent and more variable for



Fig. 7.11 Changes in total zooplankton biomass over time. See Fig. 7.6 for explanation

Fram Strait. On the other hand, the negative trend in sea-ice extent and increased temperature in the marine environment have caused declines in higher trophic levels of Arctic organisms, such as polar cod and ringed seals (*Pusa hispida*), partly because of changes in the food web and competitor populations, but also because of habitat loss with regard to Arctic seals (Renaud et al. 2012; Lydersen et al. 2014; Vihtakari et al. 2018).

7.5.4 Food-Web Effects of Changes in Zooplankton Community

Arctic zooplankton species tend to be larger and more lipid rich than their boreal congener species (Falk-Petersen et al. 2009). As planktivorous seabirds and fish species tend to be size-selective in search of prey, changes in abundance and biomass of Arctic and Atlantic species may have repercussions for the pelagic food web. For example, little auks (*Alle alle*) have a strong preference for larger *Calanus* (e.g. *C. glacialis*) and years with a dominance of the smaller *C. finmarchicus* inside the fjord may force the birds to fly longer distances to find suitable food, thereby increasing their energetic demands that in turn reduce their survival and recruitment success (Karnovsky et al. 2003; Kwasniewski et al. 2010; Hovinen et al. 2014a, b). The prey base of *C. glacialis* seems to be maintained in the Outer and Inner basins of Kongsfjorden, with highest biomass in the Inner basin. However, for visual predators it may be more difficult to selectively prey on them in the Inner basin because of turbid glacial water at the surface (Pavlov et al., Chap. 5). Other seabirds, such as

the surface feeding black-legged kittiwake, are able to change prey based on their abundance in the fjord (Vihtakari et al. 2018). The frequency of occurrence of Arctic species in seabird stomach was positively related to the sea ice index, whereas the frequency of Atlantic species increased with temperature. Thus, the negative trend in sea–ice extent and positive trend in temperature have caused increased "Atlantification" of the ecosystem in Kongsfjorden, with consequences for upper trophic levels (Vihtakari et al. 2018). In this study, we noticed such correlations for *C. finmarchicus, T. abyssorum* and krill.

However, the size structure of the zooplankton population may not only change due to changes in the species composition from larger Arctic species to smaller Atlantic species. Increased water temperature, changes in light climate and an extended productive season, due to less sea ice, can push populations towards faster development, shorter life cycles and smaller body size (Leinaas et al. 2016; Renaud et al. 2018). Calanus finmarchicus and C. glacialis are traditionally distinguished based on size classes (prosome length). Recent advances in molecular techniques have revealed larger overlap in size between the two species than previously assumed (Gabrielsen et al. 2012; Choquet et al. 2017, 2018). In particular C. glacialis may be smaller than assumed, and using size classes may therefore lead to an underestimation of C. glacialis in samples that contain both species. The extent of this bias varies with geographical location (Gabrielsen et al. 2012; Choquet et al. 2017). Along the Norwegian coast, there is a 100% overlap in size between the two species in some locations (Choquet et al. 2018), making species determination based on size highly problematic and also indicating that under increased water temperature and a prolonged primary productive season the C. glacialis population is driven to smaller body size. In Svalbard waters, the overlap is less severe (Gabrielsen et al. 2012; Choquet et al. 2017), thus using size classes will provide a realistic picture of the species composition. However, one should be aware of the potential to underestimate C. glacialis abundance and that this problem will increase with increased warming leading to a decrease in mean body size. A proper documentation of length-frequency distributions of Calanus spp. in future time-series studies may shed more light on changing size structure of the Calanus population in Kongsfjorden.

Recent years have also involved changes in the fish community in Kongsfjorden with an increased abundances of Atlantic fishes that contribute to the predation pressure on zooplankton (Szczucka et al. 2017; Vihtakari et al. 2018). This may be a response to the general increase in abundance of zooplankton, and particularly krill (Dalpadado et al. 2016). Furthermore, changes in the zooplankton species composition may affect diets of both polar cod and capelin (Hop and Gjøsæter 2013; Dalpadado et al. 2016). Nahrgang et al. (2014) found that the prey composition of polar cod differed between polar cod feeding in Arctic domains compared to those feeding in Atlantic domains such as Kongsfjorden, with the diet in the Atlantic domain being much more variable. Further warming with expansion of Atlantic water masses are also expected to extend to the northern distribution ranges for boreal fish species, which will result in increased competition with Arctic species and also increased top-down effects on the zooplankton prey (Eriksen and Dalpadado 2011; Eriksen et al. 2017).

7.6 Methodical Considerations

7.6.1 Sampling Resolution

Zooplankton, particularly in highly seasonal environments as the high Arctic, show high seasonal variability in abundance. This raises the question how representative annual sampling is. While high seasonal resolution would be preferable to address questions on phenology and life cycles, such endeavours would be logistically and financially challenging to maintain. Annual sampling in July/August has the advantage of the fjord being accessible with regard to sea-ice conditions. The pelagic ecosystem in Kongsfjorden is in a post-bloom situation mid-end July/beginning of August, with most zooplankton populations still being active in the water column. This time is also important for feeding by seabird populations around the fjord and for recruitment in fish species. Thus, monitoring the zooplankton population in July/ August provides an estimate of the available energy in the system for higher trophic levels. Part of the pelagic community inventory is missed by sampling with the MultiNet and MIK net. Tucker trawl can be used to sample zooplankton near the bottom (Hirche et al. 2016), and use of echosounders and Acoustic Doppler Profiler (ADCP) can provide additional information about temporal and spatial distribution of larger zooplankton and their diurnal vertical migrations (e.g. Darnis et al. 2017). For long-term monitoring of a system like Kongsfjorden, it is important that standardized sampling is continued annually at the same time of year, which is currently conducted as part of MOSJ (www.mosj.npolar.no). In order to determine changes over time, and for comparisons between fjords or regions, it will be important to coordinate and standardize the zooplankton sampling in different institutions and sampling campaigns. Such initiatives were discussed during a Plankton Research in Svalbard (PRiS) workshop at UNIS in 2014, but need to be implemented in future studies.

7.7 Conclusions

Zooplankton in both Kongsfjorden and the Shelf/Fram Strait area have responded to changes in fluctuating patterns in temperature related to warm-water anomalies (Beszczynska-Möller et al. 2012) as well as to decline in sea ice (Barber et al. 2015; Pavlova et al., Chap. 4), although the changes in abundance are not synchronous between Kongsfjorden and Fram Strait. Fluctuating patterns of the zooplankton composition during summer in Kongsfjorden are related to advection of Atlantic Water, particularly during winter, with an increase of some Atlantic species during warm years, but no concurrent decline in Arctic species except for the Arctic amphipod *T. libellula.* Zooplankton abundance and biomass in the fjord appear to have increased, while a similar pattern is not evident for the Shelf/Fram Strait. However, increases in Atlantic zooplankton species have been recorded after the warm 2006 in Fram Strait (Walczowski et al. 2012), and at the central HAUSGARTEN station (Kraft et al. 2012; Soltwedel et al. 2016). Within Kongsfjorden, the Atlantic *C. finmarchicus* is mainly responsible for the increasing trend in biomass and abundance, whereas *C. glacialis* has been relatively stable, possibly indicating its plasticity with regard to "Atlantification".

Data availability Zooplankton data and updated list of conversion factors are available in the MarineDatabase (Norwegian Polar Institute 2018) package for R (R Core Team 2018). The zooplankton data set in this paper is available at: https://doi.org/10.21334/npolar.2019.94b29b16.

Acknowledgements We thank the different researchers and technicians that have been involved in zooplankton collections at our sampling stations in Kongsfjorden during the 20-year time series. Olga Pavlova, Norwegian Polar Institute, is thanked for making CTD files from stations in Kongsfjorden available, and making transect plots of temperature and salinity. Padmini Dalpadado, Institute of Marine Research, is thanked for data on krill and amphipods sampled by MIK (Method Isaacs Kidd) in Kongsfjorden. MG participation was funded by the Polish Scientific Council projects: KongHau4 (W84/KongHau4/2016) and KongHau5 (W88/KongHau5/2017).

Monitoring of water masses and zooplankton in Kongsfjorden is conducted as part of Environmental monitoring of Svalbard and Jan Mayen (www.mosj.npolar.no), which currently funds the annual survey by the Norwegian Polar Institute, and as a part of Long-term studies on the Arctic marine ecosystems funded by the Institute of Oceanology Polish Academy of Sciences (IOPAN). Our sampling along the Kongsfjorden transect extends to HAUSGARTEN stations in Fram Strait when time and weather permit.

Appendix

Таха	Origin	DM conversion	References
Copepoda			
Acartia longiremis	Arctic	0.0099	1, 2, 3
Aetideidae C1–C3	Unknown	0.0696	1, 2, 3
Aetideopsis minor C4–C6	Both	0.1325	1, 2, 3
Aetideopsis rostrata C4–C6	Arctic	0.2346	1, 2, 3
Aetideus armatus C4–C6	Atlantic	0.121	
Augaptilus glacialis	Both	0.6922	1, 2, 3
Bradyidius similis C4–C6	Arctic	0.111	1, 2, 3
Calanus finmarchicus AF	Atlantic	0.2822	4, 5, 6, 7
Calanus finmarchicus AM	Atlantic	0.2139	4, 5, 6, 7
Calanus finmarchicus C5	Atlantic	0.2139	4, 5, 6, 7
Calanus finmarchicus C4	Atlantic	0.0745	4, 5, 6, 7
Calanus finmarchicus C3	Atlantic	0.0295	4, 5, 6, 7
Calanus finmarchicus C2	Atlantic	0.011	4, 5, 6, 7
Calanus finmarchicus C1	Atlantic	0.0051	4, 5, 6, 7
Calanus glacialis AF	Arctic	1.303	4, 5, 6, 7
Calanus glacialis AM	Arctic	0.6201	4, 5, 6, 7
Calanus glacialis C5	Arctic	0.6201	4, 5, 6, 7
Calanus glacialis C4	Arctic	0.1979	4, 5, 6, 7
Calanus glacialis C3	Arctic	0.0618	4, 5, 6, 7
Calanus glacialis C2	Arctic	0.0216	4, 5, 6, 7

 Table 7.8
 Abundance to dry mass conversion factors used in the study

Taxa	Origin	DM conversion	References
Calanus glacialis C1	Arctic	0.009	4, 5, 6, 7
Calanus hyperboreus AF	Arctic	3.2932	4, 5, 6, 7
Calanus hyperboreus AM	Arctic	1.2093	4, 5, 6, 7
Calanus hyperboreus C5	Arctic	1.2093	4, 5, 6, 7
Calanus hyperboreus C4	Arctic	0.3784	4, 5, 6, 7
Calanus hyperboreus C3	Arctic	0.1121	4, 5, 6, 7
Calanus hyperboreus C2	Arctic	0.0293	4, 5, 6, 8, 7
Calanus hyperboreus C1	Arctic	0.0108	4, 5, 6, 8, 7
Chiridius obtusifrons C4–C6	Both	0.2821	1, 2, 3
Copepoda nauplii	Unknown	0.0045	1, 2, 3
Disco sp. C4–C6	Unknown	0.001	
Gaetanus brevispinus C4–C6	Both	0.3392	1, 2, 3
Gaetanus tenuispinus C4–C6	Both	0.1082	1, 2, 3
Harpacticoida	Unknown	0.007	1, 2, 3
Heterorhabdus norvegicus	Arctic	0.1595	1, 2, 3
Homeognathia brevis	Atlantic	0.0069	1, 2, 3
Mesaiokeras spitsbergensis	Arctic	0.0164	1, 2, 3
Metridia longa AF	Both	0.287	9
Metridia longa AM	Both	0.137	9
Metridia longa C5	Both	0.12	9
Metridia longa C4	Both	0.034	9
Metridia longa C3	Both	0.016	9
Metridia longa C2	Both	0.007	9
Metridia longa C1	Both	0.003	9
Metridia lucens	Atlantic	0.0295	1, 2, 3
Microcalanus spp.	Both	0.007	9
Microsetella norvegica	Atlantic	0.0011	1, 2, 3
Monstrilloida C6F	Unknown	0.0595	1, 2, 3
Neomormonilla minor C5–C6	Atlantic	0.0167	1, 2, 3
Neoscolecithrix farrani C4–C6	Atlantic	0.0285	1, 2, 3
Oithona atlantica C6	Atlantic	0.0069	1, 2, 3
Oithona similis	Both	0.0025	10
Oncaea parila C6F	Arctic	0.0025	10
Oncaea spp. C6F	Unknown	0.002	10
Paraeuchaeta barbata C6F	Atlantic	9.056	1, 2, 3
Paraeuchaeta glacialis C6F	Arctic	5.907	1, 2, 3
Paraeuchaeta norvegica C6F	Atlantic	4.6717	9
Paraeuchaeta spp. AM	Both	1.7892	9
Paraeuchaeta spp. C5	Both	1.6813	9
Paraeuchaeta spp. C4	Both	0.3775	9
Paraeuchaeta spp. C3	Both	0.1215	9
Paraeuchaeta spp. C2	Both	0.0485	9

Table 7.8 (continued)

Table	7.8	(continued)
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Taxa	Origin	DM conversion	References
Paraeuchaeta spp. C1	Both	0.0384	9
Paraheterorhabdus compactus C4–C6	Both	0.0951	1, 2, 3
Pleuromamma robusta C6F	Atlantic	0.17	1, 2, 3
Pseudocalanus acuspes C6F	Arctic	0.0131	9
Pseudocalanus minutus C6F	Arctic	0.0146	9
Pseudocalanus spp. C6M	Both	0.012	9
Pseudocalanus spp. C5	Both	0.0086	9
Pseudocalanus spp. C4	Both	0.0051	9
Pseudocalanus spp. C3	Both	0.0032	9
Pseudocalanus spp. C2	Both	0.0015	9
Pseudocalanus spp. C1	Both	0.0006	9
Pseudochirella spectabilis C4–C6	Both	1.156	
Rhincalanus nasutus C4–C6	Atlantic	0.4116	1, 2, 3
Scaphocalanus brevicornis	Both	0.0333	1, 2, 3
Scaphocalanus magnus	Both	0.1593	1, 2, 3
Scolecithricella minor	Both	0.0243	1, 2, 3
Spinocalanus antarcticus	Arctic	0.0439	1, 2, 3
Spinocalanus horridus C4–C6	Arctic	0.089	1, 2, 3
Spinocalanus longicornis C6	Both	0.017	
Spinocalanus spp. C1–C6	Unknown	0.0167	1, 2, 3
Temorites brevis	Both	0.0378	1, 2, 3
Tharybidae C4-C6	Unknown	0.0186	1, 2, 3
Tharybis groenlandicus C6	Arctic	0.02	1, 2, 3
Triconia borealis C6	Arctic	0.002	10
Triconia conifera C6F	Atlantic	0.015	10
Triconia/Oncaea spp. C1–C5	Unknown	0.002	10
Undinella oblonga C4–C6	Both	0.044	
Xantharus siedleckii	Arctic	0.0239	1, 2, 3
Amphipoda		·	·
Amphipoda	Unknown	4.1089	1, 2, 3
Apherusa glacialis	Arctic	3.8947	1, 2, 3
Cyclocaris guilelmi	Arctic	1.4412	1, 2, 3
Eusirus holmii	Arctic	4.3022	1, 2, 3
Hyperia galba	Atlantic	0.9042	1, 2, 3
Hyperia medusarum	Atlantic	0.9042	1, 2, 3
Hyperiidae	Unknown	0.5715	1, 2, 3
Hyperoche medusarum	Atlantic	0.9042	1, 2, 3
Onisimus glacialis	Arctic	6.7962	1, 2, 3
Onisimus spp.	Arctic	0.227	
Scina borealis	Atlantic	0.5715	1, 2, 3
Themisto abyssorum 0-5 mm	Atlantic	0.3111	11, 12

Taxa	Origin	DM conversion	References
Themisto abyssorum 5–10 mm	Atlantic	1.4511	11, 12
Themisto libellula 0–5 mm	Arctic	3.8988	13, 12
Themisto libellula 5–10 mm	Arctic	9.5337	13, 12
Euphausiacea			
Euphausiacea calyptopis	Unknown	0.0948	1, 2, 3
Euphausiacea furcilia 0–5 mm	Unknown	0.3413	1, 2, 3
Euphausiacea furcilia 5–10 mm	Unknown	0.6614	1, 2, 3
Euphausiacea nauplii	Unknown	0.004	1, 2, 3
Meganyctiphanes norvegica	Atlantic	2.4315	
Thysanoessa inermis	Both	2.4315	14
Thysanoessa longicaudata	Atlantic	2.3183	1, 2, 3
Thysanoessa raschii	Both	2.633	
Ostracoda			
Ostracoda 0–1 mm	Unknown	0.0136	6
Ostracoda 1–2 mm	Unknown	0.0438	6
Ostracoda 2–3 mm	Unknown	0.2666	6
Ostracoda 3–5 mm	Unknown	0.429	6
Cladocera			
Evadne nordmanni	Atlantic	0.0025	18
Decapoda			
Decapoda larvae	Unknown	1.1897	1, 2, 3
Eusergestes arcticus zoea	Both	0.0713	1, 2, 3
Hyas araneus megalopa	Arctic	0.45	1, 2, 3
Hyas araneus zoea	Arctic	0.25	1, 2, 3
Hymenodora glacialis	Arctic	7.9846	1, 2, 3
Pagurus pubescens megalopa	Arctic	0.69	1, 2, 3
Pagurus pubescens zoea	Arctic	0.63	1, 2, 3
Pandalus borealis zoea	Both	4.3669	1, 2, 3
Sabinea septemcarinata zoea	Both	0.9571	1, 2, 3
Isopoda			
Bopyridae	Unknown	0.019	1, 2, 3
Isopoda	Unknown	0.019	1, 2, 3
Mysida			
Boreomysis arctica	Arctic	1.2253	15
Mysidae	Unknown	1.2253	1, 2, 3
Pseudomma truncatum	Both	1.2253	1, 2, 3
Cumacea			
Cumacea	Unknown	0.9571	1, 2, 3
Cirripedia			
Cirripedia cypris	Unknown	0.012	4
Cirripedia nauplii	Unknown	0.012	4

Taxa	Origin	DM conversion	References
Facetotecta		!	
Facetotecta nauplii	Unknown	0.012	4
Polychaeta			
Pelagobia sp.	Atlantic	0.1131	1, 2, 3
Polychaeta adult	Unknown	0.4492	1, 2, 3
Polychaeta metatrochophore	Unknown	0.0016	1, 2, 3
Polychaeta mitraria	Unknown	0.0052	1, 2, 3
Polychaeta secondary	Unknown	0.0019	1, 2, 3
Polychaeta trochophore	Unknown	0.0009	1, 2, 3
Tomopteris spp.	Atlantic	0.5382	1, 2, 3
Typhloscolecidae	Unknown	0.113	1, 2, 3
Nemertea			
Nemertea pilidium	Unknown	0.001	1, 2, 3
Bryozoa			
Bryozoa larvae	Unknown	0.001	1, 2, 3
Gastropoda			
Clione limacina veliger	Both	2.6146	16
Clione limacina 0–5 mm	Both	2.8607	16
Clione limacina 5–10 mm	Both	3.5494	16
Margarites and Velutina veliger	Unknown	0.074	1, 2, 3
Limacina helicina veliger	Both	0.257	17
Limacina helicina 0–5 mm	Both	0.8013	17
Limacina helicina 5–10 mm	Both	3.1325	17
Limacina retroversa 0–5 mm	Atlantic	0.8013	17
Limacina retroversa 5–10 mm	Atlantic	3.1325	17
Bivalvia			
Bivalvia veliger	Unknown	0.004	1, 2, 3
Echinodermata			
Echinodermata larvae	Unknown	0.001	18
Hydrozoa			
Aeginopsis laurentii 0–5 mm	Both	0.2628	1, 2, 3
Aglantha digitale 0–5 mm	Arctic	0.045	1, 2, 3
Aglantha digitale 5–15 mm	Arctic	1.4898	1, 2, 3
Botrynema ellinorae	Arctic	2.1767	1, 2, 3
Bougainvillia spp.	Arctic	2.0551	1, 2, 3
Ce-ass Dimophyes arctica	Arctic	10.3325	1, 2, 3
Halitholus cirratus	Arctic	0.305	1, 2, 3
Hydrozoa larvae	Unknown	0.0019	1, 2, 3
Hydrozoa medusae indet.	Unknown	2.1767	1, 2, 3
Nanomia cara	Arctic	3.7958	1, 2, 3
Sarsia sp.	Both	2.1767	1, 2, 3
Siphonophora	Unknown	3.7958	1, 2, 3

Taxa	Origin	DM conversion	References
Ctenophora			
Beroë cucumis	Both	0.56	1, 2, 3
Ctenophora larvae	Unknown	0.0019	1, 2, 3
Mertensia ovum	Both	1.6063	1, 2, 3
Scyphozoa	'	'	
Scyphozoa larvae	Unknown	0.56	1, 2, 3
Chaetognatha	·		
Eukrohnia hamata 0–5 mm	Both	0.0057	1, 2, 3
Eukrohnia hamata 5–10 mm	Both	0.1377	1, 2, 3
Eukrohnia hamata 10–20 mm	Both	0.9266	1, 2, 3
Eukrohnia hamata 20–30 mm	Both	6.3154	1, 2, 3
Eukrohnia hamata	Both	1.8463	1, 2, 3
Parasagitta elegans 0–5 mm	Both	0.0039	14
Parasagitta elegans 5–10 mm	Both	0.0575	14
Parasagitta elegans 10–20 mm	Unknown	0.2332	14
Parasagitta elegans 20–25 mm	Unknown	1.0556	14
Parasagitta elegans	Both	1.3572	14
Pseudosagitta maxima	Unknown	25.869	
Appendicularia	· ·	· ·	
Fritillaria borealis	Both	0.0014	1, 2, 3
Oikopleura spp. 0–5 mm	Unknown	0.001	1, 2, 3
Oikopleura spp. 5–10 mm	Unknown	0.035	1, 2, 3
Oikopleura spp. 10–20 mm	Unknown	0.4288	1, 2, 3
Oikopleura spp. 20–30 mm	Unknown	2.1989	1, 2, 3
Oikopleura spp.	Unknown	0.6659	1, 2, 3
Tunicata larvae	Unknown	0.001	
Pisces			
Pisces larvae	Unknown	6.378	19

Columns from the left: taxon, either species or a higher taxonomic rank; stage (C): adult female (AF); adult male (AM); length group (mm); biogeographic origin related to Kongsfjorden, used in classification to Arctic and Atlantic taxa; dry mass conversion factor in mg⁻¹; and source for the conversion factor. Missing reference means that an educated guess, based on a value for a similar sized species, was used as conversion factor. Entries are alphabetic within each taxonomic group

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Table 7.9 Total abund	ance (ind. m ⁻³ or in	nd. m^{-2}) and biomass	in different studies sai	mpling zooplankton ii	n Kongsfjorden, Svalbard	
References	Year (month)	Area	Gear	Zooplankton group	Abundance	Other data
Scott et al. (2000)	1997 (Aug-Sep)	Outer (Kb3)	WP2 180 µm	Calanus spp.	Calanus finmarchicus 80–207 ind m ⁻³ Calanus glacialis 13–33 ind m ⁻³ Calanus hyberboreus 15–12 ind m ⁻³	Lipid class; fatty acid
Wesławski et al. (2000)	1996 (Jul)	Inner-outer	Tucker trawl 2 mm	Macrozooplankton	Limacina helicina > 1000 ind *100 m ⁻³ Themisto libelulla > 300 ind *100 m ⁻³ *100 m ⁻³ *100 m ⁻³	Wet weight; Energy content; Length
Hop et al. (2002)	1996 (Jul, Sep) 1997 (Jul, Sep)	Inner-shelf	MultiNet 200 µm	Mesozooplankton	Jul 96, total 30–310 *1000 ind m ⁻² Jul 97, total 70–270 *1000 ind m ⁻² Sep 97, total 100–350 *1000 ind m ⁻²	Dry weight (8.8–5.1 g m ⁻²)
Kwasniewski et al. (2003)	1996 (Jul) & 1997 (Sep)	Inner	MultiNet 180 µm & WP2 180 µm	Calanus spp.	Jul 1996 Calanus finmarchicus 35–200 ind m ⁻³ Calanus glacialis 46–272 ind m ⁻³ Calanus hyberboreus 5.6 ind m ⁻³ Sep 1997 Calanus finmarchicus 103–446 ind m ⁻³ ind m ⁻³ Calanus glacialis 15–192 ind m ⁻³ Calanus hyberboreus 13.4 ind m ⁻³	

				,		
kusz et al. (2003)	2002 (Sep)	Outer	WP2 180 μm & WP3 1000 μm	Mesozooplankton	Mesozooplankton 2700 ind m ⁻³	
edow et al. (2004)	2001 (May)	Inner-shelf	MultiNet 200 µm	Mesozooplankton	Calanus finmarchicus 3–421 ind m ⁻³ Calanus glacialis 2–428 ind m ⁻³	ADCP
chka and Hagen 35)	1998–1999 (Sep–Jul)	Outer	Modified Apstein 100 µm	Small copepods	<i>Pseudocalanus minutus</i> 1088–111,297 ind m ⁻² <i>Oithona similis</i> 4483–704,633 ind m ⁻² Nauplii 31,617 ind m ⁻²	Relative stage distribution
p et al. (2006)	1996-2002	Inner-outer	MultiNet 180 µm & WP3 1000 µm	Mesozooplankton	Calanus finmarchicus 50–600 ind m^{-3} Calanus glacialis 20–330 ind m^{-3} Calanus hyberboreus 2–110 ind m^{-3} Metridia longa 1–100 ind m^{-3} Pseudocalanus sp. 35–1370 ind m^{-3} Oithona similis 75–3930 ind m^{-3} Triconia borealis 3–180 ind m^{-3}	
kusz et al. (2009)	2002 (Apr, Jul, Sep)	Inner-shelf	MultiNet 180 µm	Mesozooplankton	Apr, total 40–2010 ind m^{-3} Jul & Sep, total 410–10,560 ind m^{-3} Data on single species also included	
hholz et al. 10)	1996 & 2006	Inner-shelf	Tucker trawl 2 mm	Euphausiids	<i>Thysanoessa inermis 7</i> ind 100 m ⁻³ <i>Thysanoessa longicaudata 3</i> ind 100 m ⁻³	Total lipid
						(continued)

				,		
References	Year (month)	Area	Gear	Zooplankton group	Abundance	Other data
Willis et al. (2006)	2002 (Apr-Jun & Jul-Sep)	Outer	SAMS mooring sediment trap (65 m)	Mesozooplankton		ind/trap
Wallace et al. (2010)	2006–07 (Jun–Aug) & 2007–08 (Aug–Aug)		SAMS mooring 300-kHz ADCP & sediment trap (100 m)	Mesozooplankton	ind/trap	Absolute volume backscatter (Sv)
Daase et al. (2013)	2006 (Apr-Sep) & 2007 (May-Oct)		MultiNet 200 µm;	Calanus glacialis	2006: 233,100 ind m ⁻² (peak May) 2007: 20,000–30,000 ind m ⁻² (May–Oct)	Dry weight: 7000- 11,000 mg m ⁻² 700- 12,000 mg m ⁻²
Kwasniewski et al. (2013)	2003 (Apr-Jul) & 2004 (May-Jun)	Outer (Kb3)	WP2 180 μm & MultiNet 180 μm	Mesozooplankton	Total mesozooplankton: Early spring 788–1030 ind m ⁻³ Spring bloom 410–7065 ind m ⁻³ Summer 795–6016 ind m ⁻³	Dry weight: 23–188 mg m ⁻³
Berge et al. (2015a, b)	2013–2015 (Jan)	Outer (Kb3)	MultiNet 200 µm & MultiNet 64 µm	Mesozooplankton	Small copepods 650–2100 ind m ⁻³ <i>Calanus</i> spp. 6–15 ind m ⁻³	Respiration; ADCP
Grenvald et al. (2016)	2013 (Jan) & 2014 (Feb)	Kb3	MultiNet 200 µm & MultiNet 64 µm MIK	Micro, Meso & Macrozooplankton	Total zooplankton 64 μ m 1477–3002 ind dm ⁻³ Small copepods 300–1250 ind m ⁻³ <i>Calanus</i> 20–50 ind m ⁻³ <i>T. inermis</i> 51–1096 (Feb 2013), 1848–2536 (Jan 2014) ind m ⁻³	

(continued
Table 7.9

	Dry weight: Small 3.6 mg m^{-3} Medium 42.7 mg m^{-3} Large 39.2 mg m^{-3}
Euphausiids 0–3140 ind m ⁻² (inner) Euphausiids 4–267 ind m ⁻² (outer) Amphipods 0–3078 ind m ⁻² (inner) Amphipods 1–907 ind m ⁻² (outer)	Small zooplankton 5688 ind m ⁻³ Medium zooplankton 4131 ind m ⁻³ Large zooplankton 13 ind m ⁻³
Euphausiids & Amphipods	Small zooplankton; Medium zooplankton; Large zooplankton
MIK 1.5 mm	WP2 56 µm & MultiNet 180 µm & Tucker trawl 1 mm
Inner-outer	Outer
2006–2011	2013 (Jul)
Dalpadado et al. (2016)	Ormanczyk et al. (2017)

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