Zooplankton in Breiðafjörður: annual variability in community composition, abundance and fecundity

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Zooplankton in Breiðafjörður: annual variability in community composition, abundance and fecundity

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90 ECTS thesis submitted in partial fulfillment of a Magister Scientiarum degree in biology

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Abstract

Insights into life cycles of zooplankton, their fecundity and energy requirements, provides essential information for better understanding of energy transfer through trophic levels in the marine ecosystems. Zooplankton abundance, community composition and developmental stages of individual species of zooplankton were monitored at two locations in Breiðafjörður, West Iceland, in the summers of 2007-2009. This study revealed that the abundance of zooplankton varied between years with decreasing annual mean abundance in the three years, where the abundance in 2009 was six times lower than in 2007. The timing and magnitude of the maximum in abundance in 2007 resembled copepod life cycles of northern areas, such as Disco Bay and Tromsø, while the life cycles reflected southern areas, such as The Faroe Islands and the Western Channel in England in 2008 and 2009. Additionally, the feeding and fecundity parameters egg production and gut content (quantified as chlorophyll a) were measured for the two most abundant species of copepods, Temora longicornis and Calanus finmarchicus in 2008-2009. Gut content and egg production of T. longicornis were not correlated with phytoplankton concentration, which indicates that the females did not base their egg production solely on the phytoplankton standing stock. The gut content of C. finmarchicus in Breiðafjörður was positively correlated with chlorophyll a concentration, while egg production rate was not. Egg production rates were positively correlated with the gut content. Thus, the chlorophyll a concentration might not be the limiting factor for the egg production rate and other factors, such as dinoflagellates, flagellates and ciliates might be limiting the female egg production rate.
Útdráttur

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Þakkir


Stefáni Á. Arngrímssyni, Ásgeiri Valdimarssyni og Guðjóni Elíssyni vil ég þakka fyrir mikla og góða aðstoð á sjónum í sýnatökum. Sú aðstoð fólst meðal annars í því að leysa úr flækjum á dýrasvísfáfi, gera togin nákvæmlega eins og ég vildi auk þess að hughreista mig í sjóveikinni. Þar að auki kenndu þeir mér sjómennsku og að lesa í náttúruna. Það var ávallt skemmtilegt með ykkur á sjónum og glaðværð allsráðandi.


Hafrannsóknastofnuninni og Háskóla Íslands þakka ég fyrir not á aðstoðu, tækjum og tólum.

Vinum og samstarfsfólki hjá Vöð í gegnum tíðina vil ég senda þakkir fyrir alla aðstoð og góðar samverustundir. Þetta voru mér ömetanlegar stundir, sérstaklega fóstudagskaffið. Samstúdentum og samstarfsfólki á Aragötu 9 og í Óskju þakka ég jafnframt góðar samverustundir á námstímanum.


Verkefnið var fjármagnað af Vöð - Sjávarrannsóknasetri við Breiðafjörð, Fiskiðjunni Bylgjan í Ólafsvík, og Verkefnasjóði Sjávarútvegsins, deild um sjávarrannsóknir á samkeppnissviði.
1 Introduction

Copepods are of great importance in the oceanic food web. They are often referred to as the key species between the primary productive phytoplankton and organisms of higher trophic level (Conover and Corner 1968, Conover 1988, Kiørboe 1990, Hopcroft and Roff 1998, Head and Pepin 2010). To better understand the flow of energy through trophic levels of the oceanic ecosystem it is important to explore the life cycle of the most common groups of zooplankton and their connection with other trophic levels (Richardson et al. 1999, Hays et al. 2005, Broms and Melle 2007, Mackas and Beaugrand 2010).

In the North-Atlantic Ocean there is a great seasonal variation in physical, chemical and biological conditions. Life-cycles of copepods are well adapted to cold water and the seasonal variation in their habitats (Conover and Corner 1968). Their success might be due to their timing of reproduction and hatching of eggs to the phytoplankton spring bloom (Hirche 1996b), as well as the body shape, prey detection and the capability to have sexual reproduction in each generation (Kiørboe 2011).

Egg and nauplii stages of copepods are presumed to be important first dietary food source for pelagic fishes and as the larvae grow they tend to eat larger copepods (Kiørboe 1990, Buckley and Durbin 2006, Busch et al. 2010, Robert et al. 2011). Timing of events in copepod life cycle is, therefore, of great importance for the oceanic fish stocks. Climate changes on global scale may affect copepods variously, and e.g. have impact on timing of peaks in abundance (Mackas et al. 2012).

Recruitment of copepods depends on food availability and for most copepods, phytoplankton is considered to be the main food source (Niehoff et al. 1999, Campbell et al. 2001, Devreker et al. 2005, Debes et al. 2008). Therefore, a seasonal changes in the phytoplankton concentration and species composition is often reflected in copepod recruitment and growth (Gislason 2005, Debes et al. 2008). It has though been discussed that nutritional quality of the food particles (e.g. in terms of fatty acids) of the phytoplankton affects the egg hatching of the species (Jónasdóttir et al. 1998, Evjemo et al. 2008). In addition to the food quality, the lipid reserves from the previous summer can fuel egg production the following spring (Hirche et al. 1997, Niehoff and Hirche 2000, Koski et al. 2008). Copepods are selective in their feeding behavior, where smaller copepods (such as Acartia sp.) have showed feeding preferences for smaller phytoplankton (<20µm) where larger copepods (such as Calanus sp.) preferred larger phytoplankton (>20µm) (Lee et al. 2012).

The role of heterotrophic protists as an important food source of copepods and their effect on egg production rate has been questioned, and some studies have observed correlation between increased egg production rates of C. finmarchicus and abundance of autotrophic dinoflagellates, flagellates and ciliates (Jónasdóttir et al. 2005, Jónasdóttir et al. 2011), while Richardson et al. (1999) argued that ingestion of non-chlorophyll containing particles could have supplied the energy required for the egg production they recorded. The
relationship between phototrophs and heterotrophs heterotrophic can vary between species of copepods and reproduction of *T. longicornis* has been observed to have increased egg production rate in high concentration of chlorophyll *a* and high egg hatching rate when feeding on heterotrophic protists (Arendt et al. 2005).

Breiðafjörður is a wide open fjord located at the West coast of Iceland. The fjord is ~50 km wide and 150 km deep with bottom depth up to 200 meters, but extended areas are shallower than 20 meters. In the fjord there are many islands and reefs which create a unique ecosystem in Iceland. Due to its particular and copious biota the inner fjord shore and islands were protected in 1995 (Skarphedinsdottir and Gunnarsson 1997). Most emphasis in research in Breiðafjörður has been on vertebrates, such as birds and fishes, benthic invertebrates and kelp (Skarphedinsdottir and Gunnarsson 1997). Spawning grounds for many important pelagic fishes are found in Breiðafjörður but limited research on zooplankton has been conducted (Marteinsdottir and Astthorsson 2005) and little is known about seasonal changes in abundance and community composition of zooplankton in the fjord. However, in the years 1971-1982 zooplanktons were collected in May-June each year in the mouth of the fjord. Remarkable changes were observed in magnitude of zooplankton from year to year, in some years similar to the changes in the southwestern area of Iceland. Zooplankton distribution around Iceland was dissimilar in other years (Astthorsson and Hallgrimsson 1983). Furthermore, a small investigation was conducted in Hvammsfjörður, the innermost part of Breiðafjörður, with regular observation from the shore in 1981 to 1982 on hydrograph and zooplankton. Copepods were the most common group of zooplankton, in highest abundance in May, followed by a second peak in July (Astthorsson and Hallgrimsson 1983).

In the perspective that planktonic animals play the major link between primary producer and higher trophic levels in the oceanic environment (Kiørboe 1990), a detailed knowledge of the biological factors (such as factors controlling egg production) which influence the copepods life cycle are vital to understand their role in the pelagic system of the North Atlantic (Hirche 1996b, Richardson et al. 1999). Enhanced knowledge on those biological factors which affect the copepod life cycle is essential for improving the model prediction for the secondary production and thus understanding the energy flux through food chains (Avila et al. 2012). Such informations provide us insight into the complex, and many yet unknown details of oceanic features.

The North-Atlantic Oceanic areas are characterized by low species diversity of copepods but high abundance. The most common species offshore are *Calanus finmarchicus* (Conover 1988, Astthorsson et al. 2007, Hirche and Kosobokova 2007) but *Temora longicornis*, *Pseudocalanus* sp., *Acartia longiremis*, *Acartia clausi*, *Oithona spinirostris*, and *Oithona similis* in coastal areas (Debes and Eliassen 2006, Astthorsson et al. 2007, Dvoretzky and Dvoretzky 2009).

### 1.1 Objectives

The aim of this study was to monitor the annual variance in zooplankton community composition and abundance in Breiðafjörður, West-Iceland, with emphasis on the key
copepod species of the fjord. They are *Calanus finmarchicus*, *Temora longicornis*, *Pseudocalanus* sp. and *Acartia* sp. Furthermore the feeding and fecundity of two of the most common copepods in the bay, *T. longicornis* and *C. finmarchicus*, were estimated through two summers for determination of the annual variance in the carbon flow through copepods and the secondary production within the bay.
2 Zooplankton in Breiðafjörður: temporal variation in abundance and species composition

2.1 Introduction

Zooplankton is of great importance in the oceanic food web. It is often referred to as the key link between the primary productive phytoplankton and organisms of higher trophic levels (Conover and Corner 1968, Eriksson 1973, Conover 1988, Kiørboe 1990, Hirche 1996a, Gislason and Astthorsson 2002, Head and Pepin 2010). A detailed knowledge of the biological and physical factors which influence the life cycle of copepods is vital to understand their role in the pelagic system of the ocean (Hirche 1996b, Richardson et al. 1999, Hays et al. 2005, Broms and Melle 2007, Mackas and Beaugrand 2010).


Copepod annual mean biomass and species diversity around Iceland has been shown to be greater in coastal water compared to the open ocean, due to higher proportion of neritic species (Astthorsson and Gislason 1992, Gislason and Astthorsson 1995). Additionally, the spring spawning of *C. finmarchicus* begins earlier in shallow water (<200 m) than offshore (Astthorsson and Gislason 1999, Gislason 2005). The importance of the shallow waters to copepods could be a consequence of the relatively high annual mean phytoplankton production in coastal areas in Icelandic water (Thordardottir 1994).

Several studies have revealed the importance of phytoplankton biomass quantified as chlorophyll *a* concentration, as food availability, for abundance of copepods (Niehoff et al. 1999, Campbell and Head 2000, Maps et al. 2005, Martynova et al. 2011). At the same time, other studies have discussed that chlorophyll *a* concentration alone, is not a good predictor for egg production but other factors such as abundance of autotrophic and heterotrophic dinoflagellates, flagellates and ciliates play a significant role (Ohman and Runge 1994, Saiz et al. 2003, Jónasdóttir and Koski 2011). The vertical distribution of copepods has though been shown not to be determined by subsurface chlorophyll maximum and neither biomass nor secondary production connected to chlorophyll concentration (Koski et al. 2011). There is evidence of food concentration being the main controlling
factor of egg production of copepods while temperature is controlling only when food is not limiting, due to reduction in female size with increasing temperature and hence, egg carrying capacity (Saiz et al. 2003, Isla et al. 2008).

Breiðafjörður is a wide open bay located on the West coast of Iceland. The bay is ~50 km wide and 150 km deep with maximum bottom depth of close to 200 meters. Extended area of the bay is shallower than 20 meters, there are many islands and skerries and the tidal range in the bay ranges up to 6 meters (Icelandic hydrographic survey). Copepods are important food for survival of fish larvae (Buckley and Durbin 2006, Busch et al. 2010, Robert et al. 2011). Spawning grounds for many important pelagic fishes are found in Breiðafjörður (Marteinsdottir and Astthorsson 2005). It has been pointed out that limited research on copepods has been conducted in Breiðafjörður and further research is needed (Skarphedinsdottir and Gunnarsson 1997). Knowledge on seasonal changes in abundance and community composition of copepods in the North Atlantic Ocean is of importance for better understanding of the tropic interactions of the pelagic ecosystem. In a diverse ecosystem as the bay Breiðafjörður, where there is a great mixing of the water column, a seasonal study of copepods abundance gives an insight into the various interactions between environment and development of copepods.

The aim of the present study was to describe seasonal variability in species composition and abundance of zooplankton in Breiðafjörður. Furthermore, an emphasis was put on the life cycle strategies of four key species of copepods which dominated the copepod community in Breiðafjörður in the years 2007, 2008 and 2009. The dominant species in all years were *Calanus finmarchicus*, *Temora longicornis*, *Pseudocalanus* sp. and *Acartia* sp. The frequent sampling through the reproduction season provided a detailed image of temporal changes in the copepod community, both in terms of production capacity of the area and timing of events. During the three years of sampling, the community composition and abundance of copepods in Breiðafjörður showed annual variability.
2.2 Methods

2.2.1 Study site and sampling

Zooplankton was collected in Breiðafjörður, at one station in 2007 and two stations in 2008 and 2009. The inner station (Station 1) was located at 65°11'02"N and 22°52'92"W, with bottom depth of 45 - 50 meters, and the outer station (Station 2) at 65°04'23"N and 23°49'03"W, with bottom depth of 105–110 meters (Figure 2.1). Samples were taken during daytime with ~ten day interval, 8–15 times each year. Samples were collected from 7th June–25th September in 2007, from 15th May–31st August in 2008 and from 4th April–28th September in 2009, (Table 2.1).

Zooplankton samples were collected with WP-2 net with 0.25 m² opening and 200 µm mesh size. The net was towed vertically from 50 meters depth to surface at station 2 and from the bottom to surface at station 1. The net was towed with the speed of ~1 m s⁻¹ and the volume of water filtered was estimated with a flow-meter fitted in the mouth off the net.

Figure 2.1 Map of sampling stations in the bay Breiðafjörður in West-Iceland. Samples were collected from 15th May to 31st August in 2008 and from 4th April to 28th September in 2009. Map is redrawn from Gunnarsson 1991. The dotted lines depict the 50m depth and dashed line the 200m contour.
Onboard the vessel, the zooplankton samples were sieved through 500 μm net to remove scyphozoans and hydrozoans from the sample. The displacement volume of the zooplankton was measured in a graduated cylinder with known volume of seawater (usually around 100–200 ml). The sample was then gently transferred to a container and preserved in 4% formalin.

At the stations, YSI water profiler was used to take profiles through the water column in order to collect data on hydrographic properties of the water. Additionally seawater samples for chlorophyll a measurements were collected in order to estimate phytoplankton standing stock and the food availability of primary producers for the zooplankton (pers. comm. Erla Björk Örnólfsdóttir).

In the laboratory, samples were subsampled with a Motoda splitter (Motoda 1959). Aliquots containing ~500 individuals were identified and enumerated to lowest taxonomic level possible under a dissecting microscope. If individuals of *Calanus finmarchicus* were fewer than 200 in the subsample, aliquots were counted until a minimum of ~200 individuals were enumerated. *C. finmarchicus, Temora longicornis, Acartia* sp. and *Pseudocalanus* sp. were identified to developmental stages. Adult individuals of the genus *Acartia* sp. were identified to the species level (*Acartia longiremis* or *Acartia clausi*) but as it was difficult to identify the younger stages to species, the two species were combined for the present analysis. No attempt was made to identify *Pseudocalanus* sp. to species. Zooplankton density was standardized per m$^3$ based on the flow meter readings. Abundance per m$^3$ was converted to numbers per m$^2$ by multiplying the density estimates with the sampling depth.

### 2.2.2 Carbon

For calculations of carbon content of copepods in Breiðafjörður the copepods were divided into two groups based on size; large sized copepods were *C. finmarchicus* (all stages) and small sized copepods were *T. longicornis, Pseudocalanus* sp. and *Acartia* sp. (all stages). Number of copepods was converted into carbon by multiplying with estimated carbon weight of the group. Dry weight of large sized copepods was assumed to be 196 µg (pers. conv. Ástþór Gislason) and carbon weight of females as 50% of the dry weight (Gislason 2005). For smaller copepods no measurements are available for carbon content from Icelandic waters, therefore values from Dam and Lopes (2003) of 10.3 µg C individual$^1$ was used for calculations.

### 2.2.3 Statistics

Statistical comparison of abundance of the total zooplankton, Copepods, the four species *C. finmarchicus, T. longicornis, Acartia* sp. and *Pseudocalanus* sp. were tested against the parameters: years (2007, 2008 and 2009), temperature and chlorophyll a by linear model (LM). The data were transposed to natural logarithm plus one. The software package used was R (version 2.13.1). Full and reduced model were made for all analysis and the fitting between the models made by using chi-squared two-way ANOVA and the model with the best fit was chosen for statistical analysis. In all cases, the reduced model was at better fit.
2.2.4 Stations combined

The two sampling stations in Breiðafjörður were merged together in one data set for this analysis. The difference in abundance of zooplankton in total and copepods, both as a whole group and the most abundant species, were tested for difference between the two stations (Table 2.2.A). For total zooplankton, the group copepods and three of the key copepod species of Breiðafjörður, *C. finmarchicus*, *T. longicornis* and *Acartia* sp. the statistical test (LM) revealed no significant difference between the locations. There was though a significant difference in abundance of *Pseudocalanus* sp. between the two stations. When both of the stations were sampled in the same week, an average value of the data between the two stations was used.

<table>
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2.3 Results

2.3.1 Physical environment

The mean temperature of the upper 50 m of the water column increased from a low in April, of ~3°C, to a maximum in August, of ~10–12°C, and decreased in mid–September (Figure 2.2). The seasonal development of temperature was generally similar, while ~1.5°C higher in July–August 2008 than at the same time of year in 2007 and 2009.

Salinity changed relatively little with depth or season (data not shown). The salinity ranged from 34.2–34.9 psu during the study period and limited stratification was observed (Pers. com. Erla Björk Örnólfsdóttir).

Depth-integrated chlorophyll a (0–20 meters) concentration had one major peak during 2007, in end of May (~170 mg chl a m⁻²), followed by lower concentration throughout the summer (~45–60 mg chl a m⁻²). In 2008 the concentrations of chlorophyll a peaked by the end of May (~136 mg chl a m⁻²) while throughout rest of the summer the concentrations fluctuated (~45–91 mg chl a m⁻²). The concentrations of chlorophyll a peaked twice in 2009, at the end of May (~141 mg chl a m⁻²) and July (~148 mg chl a m⁻²) (Figure 2.3).

![Figure 2.2 Average temperature from 0–50 meter depth during 2007, 2008 and 2009. Numbers are average from measurements of both stations.](image-url)
2.3.2 Zooplankton abundance and taxonomic composition

Annual mean abundance of zooplankton in 2007 was ~990,000 individuals m\(^{-2}\), in 2008 ~380,000 individuals m\(^{-2}\) and in 2009 the annual mean abundance of zooplankton was ~160,000 individuals m\(^{-2}\). Total zooplankton abundance was significantly different between the three years (p<0.05) (Table 2.2.B). Within Breiðafjörður the zooplankton species abundance and composition varied between the years. In 2007 there was one maximum of zooplankton abundance, in end of July and was ~2,800,000 individuals m\(^{-2}\). In 2008 there was a spring maximum observed in June of ~1,200,000 individuals m\(^{-2}\), and later in the summer a maximum in end of July (~500,000 individuals m\(^{-2}\)). In 2009 there was a spring maximum noticed in May (~800,000 individuals m\(^{-2}\)) and a second maximum in July (~400,000 individuals m\(^{-2}\)) (Figure 2.4). The statistical reduced linear model (model 1, see Table 2.2.B) explained 60% of the variability in the zooplankton abundance (R\(^2\) = 0.6). In Breiðafjörður there was a significant positive correlation between abundance of total zooplankton and chlorophyll \(a\) concentration (p<0.05) as well as with temperature one week and two weeks prior to the sampling date (p<0.05).

A total of 32 species and taxonomic groups were identified in the study (Table 2.3). Seven taxa comprised the majority (83%) of the total abundance of zooplankton during the research period and thereof were five taxa of copepods, i.e. *Temora longicornis* (22%), *Calanus finmarchicus* (10%), *Pseudocalanus* sp. (17%), *Acartia longiremis* (10%), *Oithona similis* (6%). Rare species of copepods (annual mean abundance less than 50,000 individuals m\(^{-2}\)), were: *Centropages hamatus*, *Centropages typicus*, *Scolecidithricella minor*,...
Microcalanus pusillus, Metridia longa, Euchaeta norvegica, unidentified Harpacticoida and unidentified Poecilostomatoida. Copepods accounted for 60–70% of the mean annual abundance (Figure 2.4). In 2007 the abundance of copepods mean abundance was ~800,000 individuals m⁻² and abundance increased from spring to a maximum of ~2,200,000 individuals m⁻² in end of July, followed by decreased abundance through the rest of the summer. In 2008 the mean abundance of copepods was approximately 250,000 individuals m⁻² and there were two maximum in abundance of copepods, in June of ~700,000 individuals m⁻² and in July of ~750,000 individuals m⁻². In 2009 the mean abundance of copepods was 70,000 individuals m⁻² where the abundance was at maximum in May, ~160,000 individual m⁻², and in June of ~200,000 individual m⁻². The reduced model (model 2, see Table 2.2.B) explained 62% of the variability in the copepod abundance where there was positive correlation between abundance and temperature one week and two weeks prior the sampling date. Furthermore, the difference in abundance was significant between the three years (p<0.05).

Figure 2.4 Annual abundance of total zooplankton (number m⁻²) of Breiðafjörður during spring and summer of 2007, 2008 and 2009.
Table 2.2 Linear model (LM) analysis between abundance of zooplankton and environmental variables in Breiðafjörður, West-Iceland, during summers of 2007-2009 (number of observations: 54). Note that for this analysis the data from separate stations was used. T0: temperature at the day of sampling, t1-t3: temperature one to three weeks prior the sampling day, Chl a: chlorophyll a concentration, station:year: interaction between the station and year. A) Setup of the models where the copepod-figures represents which factors the variables were tested with. B) The results from the models. Level of significance: *p<0.05.

<table>
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<th>t2</th>
<th>t3</th>
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Table 2.3 Species or taxa identified in Breiðafjörður in summers 2007–2009. VC = very common species, annual mean abundance >20,000 individuals m$^{-2}$; C = common species, annual mean abundance 10,000–20,000 individuals m$^{-2}$; R = rare species, annual mean abundance <10,000 individuals m$^{-2}$.

<table>
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2.3.3 Calanus finmarchicus

The annual mean abundance of *Calanus finmarchicus* varied between years. In 2007 annual mean abundance was ~21,000 individuals m$^{-2}$, while in 2008 the annual mean abundance was ~81,000 individuals m$^{-2}$. In 2009 the annual mean abundance was ~24,000 individuals m$^{-2}$ (Figure 2.5). The difference in abundance between years was not significant (p>0.05). In 2007 the abundance of *C. finmarchicus* peaked twice, in the beginning and end of July, ~77,000 individuals m$^{-2}$ and ~33,000 individuals m$^{-2}$ respectively. Before the first peak the abundance was under 13,000 individuals m$^{-2}$, and decreased to similar number in August, after the latter peak (Figure 2.6.A). Similarly two peaks in abundance were observed in July in 2008, ~340,000 individuals m$^{-2}$ and ~260,000 individuals m$^{-2}$. Prior and after the peaks, abundance was around and below 60,000 individuals m$^{-2}$ (Figure 2.6.B). In 2009, a spring maximum of ~120,000 individuals m$^{-2}$ was observed in May and a late summer bloom in end of July and August, ~40,000 individuals m$^{-2}$ and ~34,000 individuals m$^{-2}$, respectively. In June and July the abundance was between 6,000–30,000 individuals m$^{-2}$ (Figure 2.5). The difference in abundance between years was, however, not significant (P>0.05) (Table 2.1).

Juvenile stages (stages CI–CIII), of *C. finmarchicus* were in high abundance in July 2007, ~65,000 individuals m$^{-2}$ (Figure 2.6.A) and were 85% of the total population at that time (Figure 2.7). In 2008 the juvenile stages were in high proportion in May, ~40,000
individuals m$^{-2}$ (Figure 2.6.B) which is ~75% of the total population and in July, ~250 individuals m$^{-2}$ which was 75% of the total population at that week (Figure 2.7). In 2009 abundance of juvenile stages were high in April and were ~1,800 individuals m$^{-2}$ which was 100% of the total population. In May the juveniles were in second maximum of ~100,000 individuals m$^{-2}$ and were 86% of the population (Figure 2.67). Estimated spawning time of *C. finmarchicus* was in July in 2007, in April and again in end of June/early July in 2008 and in March/April and August in 2009.

Copepodite stages CIV and CV in 2007 were in high abundance in August, ~10,000 individuals m$^{-2}$ and were 53% of the total population and again high in September when the abundance was 8,000 individuals m$^{-2}$ (Figure 2.6.A) or 100% of the population. In 2008 the copepodite stages CIV and CV were in high abundance in end of July, 170,000 individuals m$^{-2}$ (Figure 2.6.B) or 65 percent. Another maximum of 50,000 individuals m$^{-2}$ and 80% of the population was in September (Figure 2.7). The copepodite stages CIV and CV in 2009 were in maximum in May, 80,000 individuals m$^{-2}$ and were 66% of the population at that time. A second maximum in abundance of CIV and CV was in August, 30,000 individuals m$^{-2}$ (Figure 2.6.C) and accounted for 81% of the *C. finmarchicus* population.

Females of *C. finmarchicus* in 2007 were in high proportion in July, 12,000 individuals m$^{-2}$ in the beginning of the month (Figure 2.5.A), or 15% of the population, and by the end of the month the female abundance was 13,000 individuals m$^{-2}$ and 38% of the population (Figure 2.7). In 2008 the female abundance was high in July, approximately 9,000 individuals m$^{-2}$ and 54% of the total population. A second maximum was in August of 14,000 individuals m$^{-2}$ which contributed accounted for 33% of the *C. finmarchicus* population (Figure 2.7). In 2009 the abundance of females was high in June, approximately

![Figure 2.5 Total abundance (number m$^{-2}$) of Calanus finmarchicus during spring and summer 2007, 2008 and 2009.](image-url)
6,000 individuals m\(^2\) or 45\% of the population of \textit{C. finmarchicus} (Figure 2.6.C and 2.7). By the end of August there was a second maximum of female abundance of 8,000 individuals m\(^2\) which accounted for 22\% of the population of \textit{C. finmarchicus}. Males of \textit{C. finmarchicus} were only observed in beginning of June in 2007 and were \(~1,000\) individuals m\(^2\) or 9\% of the population. In 2008 the maximum of males were in July of \(~2,000\) individuals m\(^2\) and were 12\% of the population. Males of \textit{C. finmarchicus} were in maximum in June, \(~4,000\) individuals m\(^2\) and accounted for 13\% of the population. A second maximum of males were in August of 1,200 individuals m\(^2\) or 4\% of the population of \textit{C. finmarchicus} (Figure 2.6.C and 2.7).

The statistical reduced linear model (model 3, see Table 2.2) explained 13\% of the variability in the \textit{C. finmarchicus} abundance (R\(^2\) = 0.13). There was a positive correlation between abundance of \textit{C. finmarchicus} and oceanic temperature one week as well as two weeks prior to the sampling date (p>0.05).
Figure 2.6 *Abundance of all copepodite stages (number m$^{-2}$) of Calanus finmarchicus in spring and summer* A) 2007, B) 2008 and C) 2009. *Figure legend:* CI-CV: first to fifth copepodite stage of development, C6f: adult females, C6m: adult males.
There was an order of magnitude change in abundance of *Temora longicornis* between years. Annual mean abundance of *T. longicornis* in 2007 was ~280,000 individuals m$^{-2}$. In 2008 the mean abundance was ~90,000 individuals m$^{-2}$ and in 2009 the annual mean abundance was ~12,000 individuals m$^{-2}$ (Figure 2.8). Between the three years there was a significant difference in abundance of *T. longicornis* (p<0.05) whereas abundance in 2007 was highest and lowest abundance in 2009. In 2007 the abundance of *T. longicornis* increased from June of ~40,000 individuals m$^{-2}$ until the abundance reached a maximum in end of July, ~700,000 individuals m$^{-2}$. In August and through September the abundance decreased rapidly and was ~2,000 individuals m$^{-2}$ in end of September (Figure 2.9.A). In 2008 the abundance increased from May, of ~10,000 individuals m$^{-2}$, until the abundance reached a maximum in June of ~400,000 individuals m$^{-2}$, and decreased thereafter to ~5,000 individuals m$^{-2}$ in mid-July. A Second peak was observed in end of July, of ~150,000 individuals m$^{-2}$, and decreased to less than 500 individuals m$^{-2}$ in mid-September (Figure 2.9.B). In 2009 the abundance of *T. longicornis* was low through April until mid-May, less than 5,000 individuals m$^{-2}$, and reached maximum in June, of ~120,000 individuals m$^{-2}$. In end of June the abundance was less than 100 individuals m$^{-2}$. A second maximum in 2009 was observed in mid-July of ~30,000 individuals m$^{-2}$. For the rest of the summer the abundance was less than 5,000 individuals m$^{-2}$ (Figure 2.9.C). There was a positive
correlation between abundance of *T. longicornis* and chlorophyll *a* concentration within Breiðafjörður (p<0.05)

Juvenile copepodite stages (CI–CIII) of *T. longicornis* in 2007 were in maximum in July and were ~100,000 individuals m⁻² and accounted for 18% of the population. In 2008 the juvenile copepodite stages (CI–CIII) were in maximum in June and were 160,000 individuals m⁻² and accounted for 38% of the population. In 2009 the juvenile copepodite stages (CI–CIII) were in high proportion in April and accounted for 50% of the population although the abundance was 100 individuals m⁻². By mid-May the abundance was 5,000 individuals m⁻² and accounted for 4% of the *T. longicornis* population (Figures 2.9 and 2.10).

Copepodite stages CIV and CV in 2007 were in high abundance in July, ~165,000 individuals m⁻² and were 30% of the population. In 2008 the copepodite stages CIV and CV were in ~90,000 individuals m⁻² in July and accounted for 21% to the population. By August a second maximum was in abundance of CIV and CV of 42,000 individuals m⁻² which accounted for 79% of the *T. longicornis* population at that time. In 2009 the abundance of CIV and CV stages was ~112 individuals m⁻² in April and accounted for 50% of the population. By June the abundance was 3,000 individuals m⁻² and was in 11% proportion of the population. In end of August the abundance of CIV and CV stages was ~1,000 individuals m⁻² which accounted for 23% of the population. Female abundance in 2007 was at maximum in the beginning in August, of 340,000 individuals m⁻² which accounted for 48% of the population at that time. In 2008 a maximum in abundance of females was in June of 80,000 individuals m⁻² which accounted for 19% of the population. A second maximum was in July, 57,000 individuals m⁻² or 43% of the population. Female abundance

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**Figure 2.8** Total abundance (number m⁻²) of *Temora longicornis* during spring and summer 2007, 2008 and 2009.
in 2009 was negligible in April and by May the female abundance was at maximum of 62,000 individuals m\(^{-2}\) which was 50% of the *T. longicornis* population at that time. Males of *T. longicornis* were in 2007 in high abundance in July, 150,000 individuals m\(^{-2}\) which accounted for 37% of the population and in August of 230,000 individuals m\(^{-2}\) and accounted for 48% of the population. In 2008 a maximum in abundance was in June of 90,000 individuals m\(^{-2}\) and which was 22% of the population. By end of August the males were negligible. In 2009 the male abundance was negligible in April and at maximum in May of 55,000 individuals m\(^{-2}\) and 44% of the population. By July the males abundance was low for the remaining of the summer (Figures 2.9 and 2.10).

The statistical reduced linear model (model 4, see table 2.2) explained 52% of the variability in the abundance of *T. longicornis* \((R^2 = 0.52)\). A positive correlation was between abundance of *T. longicornis* and temperature two weeks prior the sampling date \((p>0.05)\).
Figure 2.9 Abundance of all copepodite stages (number m$^{-2}$) of Temora longicornis in spring and summer A) 2007, B) 2008 and C) 2009. Figure legend see Figure 2.6.
Figure 2.10 Seasonal changes in relative abundance of developmental stages of *Temora longicornis* during 2007, 2008 and 2009. Figure legend, see Figure 2.6.

### 2.3.5 *Pseudocalanus* sp.

Between the two stations which were sampled in Breiðafjörður was a significant difference in abundance of *Pseudocalanus* sp. where higher abundance was at station 1 than at station 2 (p<0.05). This difference between stations was observed in both years 2008 and 2009, while in 2007 samples were only collected at station 1.

Abundance of *Pseudocalanus* sp. in 2007 was an order of magnitude higher than for the other two years, the abundance though, between 2008 and 2009 was significant (p<0.05). In 2007 the annual mean abundance of *Pseudocalanus* was ~300,000 individuals m$^{-2}$, the mean abundance in 2008 was ~17,000 individuals m$^{-2}$ and in 2009 the annual mean abundance was ~4,500 individuals m$^{-2}$ (Figure 2.11). In 2007 the abundance of *Pseudocalanus* pp. increased steadily from June, from ~30,000 individuals m$^{-2}$, until beginning of August when the abundance reached ~900,000 individuals m$^{-2}$. Throughout August and September the abundance decreased and was ~90,000 individuals m$^{-2}$. Throughout August and September the abundance decreased and was ~90,000 individuals m$^{-2}$ until the end of September (Figure 2.12.A). In 2008 the abundance increased from May, of ~2,000 individuals m$^{-2}$, to June, from ~37,000 individuals m$^{-2}$, which was the abundance maximum measured. In July the abundance decreased to ~300 individuals m$^{-2}$. A second peak was observed in July, of ~60,000 individuals m$^{-2}$ and decreased steadily until September when the abundance was less than 500 individuals m$^{-2}$ (Figure 2.12.B). In 2009 the abundance increased from April, of ~2,000 individuals m$^{-2}$ until end of May when a maximum of ~21,000 individuals m$^{-2}$ was observed. A second maximum was observed in end of June, of
~36,000 individuals m$^{-2}$. For the rest of the summer the abundance of *Pseudocalanus* sp. was below 6,000 individuals m$^{-2}$ (Figure 2.12.C).

![Figure 2.11 Total abundance (number m$^{-2}$) of *Pseudocalanus* sp. during spring and summer 2007, 2008 and 2009.](image)

Juvenile copepodite stages (CI–CIII) of *Pseudocalanus* sp. in 2007 were ~11,000 individuals m$^{-2}$ in June who accounted for 40% of the population at that time and the abundance reached a maximum of 125,000 individuals m$^{-2}$ in August which was 14% of the total population. In 2008 the juvenile stages (CI–CIII) were at maximum in July of ~42,000 individuals m$^{-2}$ which accounted for 71% of the population. In 2009 the juvenile copepodite stages (CI–CIII) were in high abundance in June, of ~8,000 individuals m$^{-2}$ which accounted for 22% of the population. Copepodite stages CI and CV were in 2007 in high abundance in August, of ~400,000 individuals m$^{-2}$ which accounted for 45% of the population. In 2008 the abundance of copepodite stages CIV and CV was high in June, ~13,000 individuals m$^{-2}$, which accounted for 36% of the population, and in July, 18,000 individuals m$^{-2}$ which accounted for 53% of the population. In 2009 the CIV and CV abundance was high in June, ~14,000 individuals m$^{-2}$ which was 39% of the *Pseudocalanus* sp. population. Abundance of females was in 2007 highest in the beginning of August, of ~280,000 individuals m$^{-2}$ which accounted for 30% of the population at that time. In 2008 the female abundance was at maximum in end of June, ~14,000 individuals m$^{-2}$ which accounted for 38% to the population of *Pseudocalanus* sp. at the time. A second maximum was in August, ~11,000 individuals m$^{-2}$ which accounted for 47% of the population. In 2009 the female maximum abundance was in end of May, ~5,000 individuals m$^{-2}$ which was 24% of the population and maximum was again in June, ~7,000 individuals m$^{-2}$ which accounted for 18 percent of the population. The abundance of males in 2007 was high in August, ~100,000 individuals m$^{-2}$ which was 11% of the population. In 2008 the male abundance was at maximum in May, ~5,000 individuals m$^{-2}$ which accounted for 39% of the population. In 2009 the abundance
of males was at maximum in June ~8,000 individuals m\(^{-2}\) which accounted for 21\% to the population of *Pseudocalanus* sp (Figure 2.13).

The statistical model chosen was reduced model (model 5, see table 2.2) which explained 68\% of the variation (\(R^2 = 0.68\)). There was no significant correlation between *Pseudocalanus* sp. and the environmental factors tested (table 2.2).
Figure 2.12 Abundance of all copepodite stages (number m$^{-2}$) of Psuedocalanus sp. in spring and summer A) 2007, B) 2008 and C) 2009. Figure legend see Figure 2.6.

Figure 2.13 Seasonal changes in relative abundance of developmental stages of Pseudocalanus sp. during 2007, 2008 and 2009. Figure legend, see Figure 2.6.
2.3.6 *Acartia* sp.

*Acartia* sp. genus consisted of two species, they were *Acartia longiremis* which accounted for ~80–90% of the genera and *Acartia clausi* which comprised the remaining 10–20% of the genus within Breiðafjörður during 2007–2009. Because of difficulties in identifying *Acartia* species for all copepodite stages during routine sample examination, the description of these copepods was only carried out to the genera level.

There was a significant difference in abundance between the three years (p<0.05) where the abundance of *Acartia* sp. in 2007 was highest, ~180,000 individuals m$^{-2}$, while in 2008 the annual mean abundance was ~36,000 individuals m$^{-2}$ and in 2009 the mean abundance was ~10,000 individuals m$^{-2}$ individuals m$^{-2}$ (Figure 2.14). In 2007 the abundance of *Acartia* sp. was ~40,000 individuals m$^{-2}$ in June and increased to a maximum in mid-July, of ~270,000 individuals m$^{-2}$. A second maximum was in beginning of August, of ~420,000 individuals m$^{-2}$. By the end of September the abundance was back to relatively low density, of ~40,000 individuals m$^{-2}$ (Figure 2.16.A). In 2008 abundance of *Acartia* sp. was ~6,000 individuals m$^{-2}$ in the end of May, and increased to a maximum in June, of ~150,000 individuals m$^{-2}$, after which the abundance decreased down to 14,000–45,000 individuals m$^{-2}$ through July to mid–August. In September the abundance was below 2,000 individuals m$^{-2}$ (Figure 2.16.B). In 2009 *Acartia* sp. abundance was below ~5,000 individuals m$^{-2}$ in April. A maximum was observed in May, of ~40,000 individuals m$^{-2}$. In mid-June the abundance was between 20,000–25,000 individuals m$^{-2}$. A second maximum was noticed in end of July, of ~15,000 individuals m$^{-2}$ and a third maximum in September, of ~26,000 individuals m$^{-2}$ (Figure 2.16.C). There was a significant positive correlation between abundance of *Acartia* sp. and chlorophyll a concentration at the time of sampling (p<0.05).

![Figure 2.14 Total abundance (number m$^{-2}$) of Acartia sp. during spring and summer 2007, 2008 and 2009.](image)

Figure 2.14 Total abundance (number m$^{-2}$) of *Acartia* sp. during spring and summer 2007, 2008 and 2009.
Juvenile copepodite stages (CI–CIII) of *Acartia* in 2007 were at maximum abundance in July, 52,000 individuals m\(^2\), which accounted for 20% of the population, and a second maximum was observed in August of 38,000 individuals m\(^2\) which accounted for 9% to the population. In 2008 juvenile copepodite stages (CI–CIII) were ~20,000 individuals m\(^2\) in June, which accounted for 47% of the population followed by a second maximum in end of July of 8,000 individuals m\(^2\) which accounted for 21% to the population. In 2009 the juvenile stages were ~8,000 individuals m\(^2\) in May, which accounted for 21% of the population, and in July the abundance of stages CI–CIII was ~3,000 m\(^2\) and accounted for 10% to the population. In 2007, abundance of copepodite stages CIV–CV was 130,000 individuals m\(^2\) in August, which was 31% of the population. In 2008 the abundance of copepodite stages CIV–CV were 71,000 individuals m\(^2\) in June and accounted for 47% of the population. In 2009 the stages CIV–CV were in high abundance in May 14,000 individuals m\(^2\) which accounted for 38% of the population of *Acartia* sp. Female abundance of *Acartia* sp. in 2007 was at maximum in August, of 200,000 individuals m\(^2\) which was at that time 48% of the population. In 2008 the female abundance was 40,000 individuals m\(^2\) in June, and accounted for 26% to the population. In 2009 the female abundance of *Acartia* sp. was at maximum in May, of 12,000 individuals m\(^2\) and accounted for 33% of the total abundance, and a second maximum in June of 12,000 individuals m\(^2\) of which accounted for 59% to the population. Males in 2007 were at maximum in July of 65,000 individuals m\(^2\) which was 23% of all *Acartias*. In 2008 the male abundance was at a maximum in June of 19,000 individuals m\(^2\) and accounted for 13% of the population, and a second maximum in July of 18,000 individuals m\(^2\) which accounted for 44% of the population at that time. In 2009 the male abundance was at maximum in June of 9,000 individuals m\(^2\) and accounted for 34% of the population (Figure 2.15).

The statistical reduced linear model (model 6, see table 2.2) explained 55% of the variability in abundance of *Acartia* sp. (R\(^2\) = 0.55). There was a significant positive correlation between chlorophyll *a* concentration and abundance of *Acartia* sp. (p<0.05).
Figure 2.15 Seasonal changes in relative abundance of developmental stages of *Acartia* sp. during 2007, 2008 and 2009. Figure legend, see Figure 2.6.
Figure 2.16 Abundance of all copepodite stages (number m$^{-2}$) of Acartia sp. in spring and summer A) 2007, B) 2008 and C) 2009. Figure legend see Figure 2.6
2.3.7 Carbon availability

Carbon availability from copepods in Breiðafjörður was on average 4500 mg C m\(^{-2}\) in 2007. The carbon from copepods during 2007 was primarily from small sized copepod species, which accounted for 50–90% of the total carbon or around 3600 mg C m\(^{-2}\) while large copepods consisted the remaining, or 900 mg C m\(^{-2}\) on average through the summer. On average, the carbon availability in 2008 in Breiðafjörður was 4800 mg C m\(^{-2}\) where large where larger copepods were the main contributors and consisted of 3500 mg C m\(^{-2}\) on average and the smaller copepods of 1300 mg C m\(^{-2}\) throughout the summer. In May and June small sized copepods were the main carbon contributors and accounted for 60–85%, while in July there was a shift in the community composition and large copepods were the main contributors for the remaining of the summer, or 80–90%. In 2009 the carbon availability from copepods was on average 2300 mg C m\(^{-2}\) through the summer, whereas large copepods accounted for 60–90% or around 1800 mg C m\(^{-2}\), while small sized copepods accounted for the remaining 10–40%, ~500 mg C m\(^{-2}\) (Figure 2.17).

![Figure 2.17 Carbon availability from copepods in Breiðafjörður during spring, summer and autumn of 2007–2009. Copepods were separated into two groups, large sized which was C. finmarchicus and small sized which consisted of T. longicornis, Pseudocalanus sp. and Acartia sp.](image)

2.3.8 Other groups

Other common groups were cladocerans, cirripedes and molluscan larvae, cladocerans accounting for ~11% of the annual mean abundance of zooplankton, although in some weeks of the year they comprised up to ~50% of the total number of animals. Cirripedes and molluscan larvae occurred in variable proportions throughout the study season cirripedes accounted for 5–30% and molluscan larvae represented 5–20% of the total number of individuals.
Annual mean abundance of cladocerans was on average 37,000 individuals m\(^2\) in 2007, in 2008 the abundance was on average 63,000 individuals m\(^2\) and in 2009 27,000 individuals m\(^2\). In 2007 and 2009 the abundance of cladocerans was high in July while in 2008 the abundance was high in May.

Cirripedes annual mean abundance was on average 31,000 individuals m\(^2\) in 2007, in 2008 the abundance was on average 16,000 individuals m\(^2\) and in 2009 the annual abundance was 45,000 individuals m\(^2\). The abundance of Cirripedes was high in end of May and early June all the three years.

Molluscans annual mean abundance in 2007 was on average 73,000 individuals m\(^2\), in 2008 annual mean abundance was 4,000 individuals m\(^2\) and in 2009 the mean abundance was 6,000 individuals m\(^2\). Molluscans were in high abundance in mid-summer all the three years.
2.4 Discussion

Copepods were by far the most abundant group of zooplankton in Breiðafjörður during 2007, 2008 and 2009, where *Temora longicornis* dominated the copepod community, followed by *Pseudocalanus* sp., *Calanus finmarchicus* and *Acartia* sp. The copepod composition in Breiðafjörður is consistent with what previously has been observed in coastal areas and fjords around Iceland and in coastal areas and fjords of the North Atlantic Ocean (Fransz et al. 1991, Gislasd and Astthorsson 1995, Halvorsen and Tande 1999, Gislasd and Astthorsson 2004, Madsen et al. 2008, Eloire et al. 2010). The relatively large copepod *C. finmarchicus* was in high proportion during spring and late summer within Breiðafjörður in 2007, 2008 and 2009. *C. finmarchicus* is found in high abundance all around Iceland in summer time and often dominates the copepod biomass in coastal areas (Astthorsson and Gislasd 1992, Astthorsson and Gislasd 1999, Gislasd and Astthorsson 2000).

*T. longicornis* is a species in low abundance in the shelves in north of Iceland while common on the southern and southwestern shelves. The magnitude of *T. longicornis* in Breiðafjörður was though high in Breiðafjörður compared to what has previously been recorded at the south coast of Iceland (Astthorsson and Gislasd 1992, Kaasa and Gudmundsson 1994, Gislasd and Astthorsson 1995, Astthorsson and Gislasd 1999, Gislasd and Astthorsson 2004).

There is a latitudinal variability in the timing of maximum abundance of *Pseudocalanus* sp. and *Acartia* sp. in the North Atlantic Ocean, wherein northern areas, *Pseudocalanus* sp. and *Acartia* sp. have late summer or autumn maximum (Krause et al. 1995, Halvorsen and Tande 1999, Madsen et al. 2008). In southern areas on the other hand, the two species have a spring or early summer maximum (Eriksson 1973, Debes et al. 2008, Eloire et al. 2010). In previous studies on seasonal development of the copepod community around Iceland, *Acartia* sp. and *Pseudocalanus* sp. have shown north- and southern division, with spring and mid-summer maximum in the south while the maximum in north occurs in midsummer and autumn (Gislasd and Astthorsson 1995, 1998a). When compared with the results of *Pseudocalanus* sp. and *Acartia* sp. from Breiðafjörður, the seasonal development in year 2007 resembled the northern areas of the North-Atlantic Ocean with one maxim in late summers while the years 2008 and 2009 resembled the southern more areas of the North-Atlantic Ocean with maximum in early summer.

Abundance of copepods in Breiðafjörður was related to previous temperature of the ocean, where abundance increased in correlation with increased temperature. On species level, abundance of *C. finmarchicus*, *T. longicornis* and *Pseudocalanus* sp. were all correlated with previous oceanic temperature. Although, *Acartia* sp. was unlike the other species, where there was no connection between abundance and temperature. The lack of correlation could be due to variability in temperature preferences of the two genera of *Acartia* sp. found in Breiðafjörður, *Acartia longiremis* and *A. clausi*, where the former species often dominates in colder waters and the latter species is in high abundance in warmer water (Eriksson 1973). Temperature in Breiðafjörður while the study was conducted was, according to daily measurements at a station in the fjord (http://www.hafro.is/Sjora/siritar/flatey.php), similar through the three years and maximum
temperature difference between the three years was around 1°C. In the three years the copepod abundance was not significantly different. Temperature in Breiðafjörður was highest in end of July and through August, with a 4-5 degree warming through summer.

Copepod recruitment depends greatly on food availability and phytoplankton is often considered to be the main food source (Campbell et al. 2001, Devreker et al. 2005). Therefore, a seasonal change in the phytoplankton concentration and species composition is often reflected in copepod recruitment and growth (Gislason 2005, Debes et al. 2008). In Breiðafjörður the abundance of T. longicornis and Acartia sp. were related to the chlorophyll a concentration of the ocean, while abundance of C. finmarchicus and Pseudocalanus sp. was not correlated with the phytoplankton abundance. Food availability and feeding rates of the species can have a major role in affecting the species abundance which is reflected in egg production of the species. Egg production of Acartia sp. and T. longicornis has previously been detected to increase with increased chlorophyll a concentration while egg production of C. finmarchicus and Pseudocalanus sp. have not been directly related to chlorophyll a availability. Heterotrophic dinoflagellates and ciliates appear to be highly relevant in the composition of copepod diets, and thus the lack of correlation between the feeding environment (in terms of chlorophyll a) and abundance (Saiz and Calbet 2011). Thus, in Breiðafjörður other food particles than observed in this study might have been favorable for C. finmarchicus and Pseudocalanus sp. and thus the lack of correlation to chlorophyll a concentration.

For all the four species of the key copepods in Breiðafjörður, an annual variation was in the maximum abundance of young stages (CI–CIII). Spawning of the copepods occurred thus at different times in the three years. The species composition and abundance of copepods in Breiðafjörður switched between the three years, whereas total abundance of all groups was high in 2007 and significantly lower in 2008 and 2009. In 2007 the dominating species were T. longicornis, Pseudocalanus sp. and Acartia sp. In 2008 both T. longicornis and Acartia sp. were in high abundance in early summer, whilst later in the summer C. finmarchicus was dominating the copepod community. In 2009 C. finmarchicus and T. longicornis were in high abundance in spring, while Pseudocalanus sp. and Acartia sp. were in minimum. The switch between the three years in the species composition may reflect the difference in life strategies of the species and react to the environment (Jespersen 1940, Debes and Eliasen 2006). The copepods must deal with an environment which can be both prolonged and extreme, which can lead to great seasonal and annual fluctuations in population composition and thus, both environmental and zooplankton cycles varies between years (Mackas et al. 2012).

The spawning period of C. finmarchicus in Breiðafjörður was similar to what has previously been studied in coastal areas around Iceland and it has been shown that the timing can vary between years (Gislason and Astthorsson 1996, 1998b, 2000). The role of variable generation cycle is unknown for Icelandic areas but in the North Sea the reproduction was controlled by quality of food and changes in body size (Koski et al. 2011).

During the study period, there was an order of magnitude difference in abundance of carbon availability from both small and large copepods. The maximum abundance varied between the years for both groups, there was thus, an annual variation in both timing and magnitude of carbon availability in Breiðafjörður during the summers of 2007–2009. Recruitment success of marine fish populations are often connected with the copepod abundance since
copepods are one of the main food sources for pelagic fish and their larvae (Buckley and Durbin 2006, Busch et al. 2010, Robert et al. 2011). The timing of fish spawning and maximum in carbon from small sized copepods and later on, large sized copepods could therefore be in a mismatch to fish larvae in some years. The size distribution and lipid content of the copepods can have impact on recruitment of fishes, for example in the North Sea cod recruitment was not correlated with abundance of Pseudocalanus sp. while there was a connection to abundance of C. finnarchicus when the species accounted for greater than 50 percent to the copepod community (Baugrand and Kirby, 2010).

The timing and magnitude of the major peaks in abundance of all the four species in Breiðafjörður varied between the three years. On one hand, in 2007 the timing of maximum abundance resembled copepod life cycles of Disco Bay, Tromsø and the North Sea, with maximum in the autumn (Fransz et al. 1991, Halvorsen and Tande 1999, Madsen et al. 2008). On the other hand in the years 2008 and 2009 the timing of maximum abundance was consistent with the timing of peaks in areas of Plymouth, The Faroe Island and Kattegat (Eriksson 1973, Debes et al. 2008, Eloire et al. 2010) whereas peak abundance was in spring and early summer.

### 2.5 Conclusion

The emphasis of this study was on four of the most abundance species of copepods in Breiðafjörður, Calanus finnarchicus, Temora longicornis, Pseudocalanus sp. and Acartia sp., and their variability in both seasonal and annual context. In this data analysis a spatial variability was excluded to simplify the data and put more detailed focus on the seasonal and annual variation, but further analyses of the spatial variability in Breiðafjörður could be of a great interest.

In Breiðafjörður the oceanic environment is constantly changing due to e.g. wind effects and oceanic currents. This frequent mixing of the fjord might cause rapid mixing and dilution of nutrients, resulting in shorter timescale of events than occurs in open ocean areas. Due to these rapid changes in Breiðafjörður samples in this research were taken every 10th day, but samples taken more frequently could give more detailed picture of the changes in copepod community of Breiðafjörður, as well as better correlation with environmental factors. Furthermore, daily measurements of temperature and salinity in the fjord would help determining the rapid changes of the fjord.

Due to dynamics in the ecosystem of Breiðafjörður and rapid changes within it, the copepod community within the bay could be an indicator for the tolerance limit of the species in relation to changes in the food environment and temperature.

Due to dynamics in the ecosystem of Breiðafjörður and rapid changes within it, the copepod community within the bay could be an indicator for the tolerance limit of the species in relation to changes in the food environment and temperature. A mesocosm where the various components affecting the copepod community of the bay would be tested individually and mixed could provide a detailed image of the factors affecting the secondary production within such as diverse ecosystem as Breiðafjörður is. Furthermore, in times when strong evidence is for systematic changes in planktonic abundance and community
structure, the bay could be used as a case study are for the tolerance of copepods and reactions in a changeable environment (Hays et al. 2005).
3 Feeding and fecundity of two key species of copepods, *Temora longicornis* and *Calanus finmarchicus*, in Breiðafjörður, West Iceland.

3.1 Introduction

Copepods are of a great importance as secondary producers in the pelagic ocean. Several factors can affect the secondary production of copepods, and it has been proposed that if one is limited, it might limit the production of a population in a whole area (Jónasdóttir et al. 2005). Those controlling factors can be e.g. food quality and food quantity, which are often affected by hydrology and seasonal fluctuations (Conover and Corner 1968, Harris and Paffenhofer 1976, Hirche 1996b, Jónasdóttir et al. 2002). Adult females of copepods do not grow somatically but invest all surplus energy into the egg production, which is therefore is considered to be representative of the juvenile growth (assuming that females and juvenile stages have same feeding rate) and is therefore used as an indicator of the population production (Hirche 1996b). Specific growth rate of females has been measured to be around 33 – 35% off gross growth efficiency (Checkley 1980, Kjørboe 1989, Hansen et al. 1997). With extensive spatial and temporal knowledge on copepods reproduction biology, such as egg production rates, percentage of spawning females, feeding and carbon demands in temperate oceanic environment, species reproduction response to various environmental factors can better be predicted.

Two of the important species of Calanoida copepods in the North Atlantic ecosystem and around Iceland, are the oceanic species *Calanus finmarchicus* (Jespersen 1940, Astthorsson and Hallgrímsson 1983, Conover 1988, Gislason and Astthorsson 1995, Astthorsson et al. 2007) and the small coastal species *Temora longicornis* (Fransz et al. 1991, Gislason and Astthorsson 1995, Krause et al. 1995, Gislason and Astthorsson 2004). Around Iceland *C. finmarchicus* often accounts for 60–80 % of the zooplankton community and the species dominates in terms of biomass (Astthorsson and Gislason 1992, Gislason and Astthorsson 1998a, Astthorsson and Gislason 1999, Gislason and Astthorsson 2002). In coastal areas off South and South-West of Iceland, the small copepod *T. longicornis* can account for up to 50% of the total copepod community (Astthorsson and Gislason 1992, Gislason and Astthorsson 1996). However, outside of the shelf and in the coastal areas north of Iceland, *T. longicornis* represents about one percent of the zooplankton abundance (Kaasa and Gudmundsson 1994, Gislason and Astthorsson 1996, 1998a, 2004).

Several studies on egg production and feeding, based on gut content of *C. finmarchicus* reveal a close correlation between chlorophyll *a* and reproductive biology of *C.
finmarchicus (Niehoff et al. 1999, Campbell and Head 2000, Gislason et al. 2008) At the same time, other studies have discussed that chlorophyll \( a \) concentration alone, is not a good predictor for egg production of \( C. \) finmarchicus and other factors such as ciliates and lipid reserves play an important role in egg production (Ohman and Runge 1994, Nejstgaard et al. 1997, Jónasdóttir et al. 2008). Research on the shelf area in the North Atlantic Ocean, have shown that \( T. \) longicornis often has a maximum in fecundity prior to the spring bloom and not coupled with the chlorophyll maximum (Devreker et al. 2005, Arendt et al. 2006). Furthermore, it has been argued that heterotrophic protists (e.g. ciliates) are of great importance for reproduction of \( T. \) longicornis (Arendt et al. 2006, Evjemo et al. 2008). In the oceanic areas off Iceland, studies on egg production rates and carbon demand for egg production of \( T. \) longicornis are limited and little is known about the factors controlling reproduction of the species. Thus, there is a spatial variability in proportional abundance of \( T. \) longicornis and \( C. \) finmarchicus between areas in Iceland. Furthermore, the egg production rates are controlled by different factors which can be spatial and vary between years and thus annual fluctuations can be expected.

Copepods are considered to be important in the secondary production of the pelagic marine ecosystem, both in terms of magnitude and biomass. The diet of copepods is commonly diverse and reflect the complexity of the pelagic food web (Kleppel 1993). The length, magnitude and timing of phytoplankton blooms can generate considerable temporal variability in copepod secondary production and eventually affects the production at higher trophic levels (Buckley and Durbin 2006, Busch et al. 2010, Robert et al. 2011). Understanding of the details in dynamic of the system and the carbon flow through each trophical level is fundamental for further knowledge on the energy flow through the food chains of the ocean (Avila et al. 2012).

Breiðafjörður is a wide open bay located on the West coast of Iceland. The bay is ~50 km wide and 150 km deep with maximum bottom depth of ~200 meters. Extended area of the bay is shallower than 20 meters, there are many islands and skerries and the tidal range in the bay is up to 6 meters (Icelandic hydrographic survey). Those characteristics of the bay may cause great mixing of the water column, increase turbidity, and consequently homogenize the nutrient concentration in the water column. The area is therefore of a great interest for studies on the biological production of the pelagic part of the ecosystem, such as copepods, in a bay of very limited stratification.

The objectives of the study was to characterize the carbon requirements and egg production of the two key copepod species, \( T. \) longicornis and \( C. \) finmarchicus, in Breiðafjörður, in relation to seasonal variation in female abundance and feeding.
3.2 Methods

3.2.1 Study site and sampling

Zooplankton was collected at two stations in Breiðafjörður in the years of 2008 to 2009. The inner station (Station 1) is at 65°11’02”N and 22°52’92”W, with bottom depth of 45–50 meters, and the outer station (Station 2) is at 65°04’23”N and 23°49’03”W, with bottom depth of 105–110 meters (Figure 3.1). Samples were taken during daytime with ~ten days interval, in the time periods of 15th May to 31st August 2008 and 4th April to 28th September 2009. In all, 8 surveys were conducted in 2008 but in 2009 the surveys were 15. For this analysis data have been combined for the two locations by the week of the year, since no significant difference in abundance was between the two stations (Sigurðardóttir, unpublished). For temperature based calculations, the average in situ temperature of the water column on the day of sampling was used.

3.2.2 Egg production

Zooplankton samples were collected with WP-2 net; with opening of 0.25 m² and 200 µm mesh size. The net was towed vertically from bottom to surface at Station 1 and from 50 meters depth to surface at Station 2. The net was towed up at a speed of ~0.2 m s⁻¹ to collect as many animals as possible and was fitted with non-filtering cod end to minimize damage to the zooplankton. Once the net was on board the zooplankton was gently transferred from the cod end into a 25 liter cooler, filled with seawater from 20 meters. The zooplankton was kept in the cooler until

In the lab swimming and intact, both externally and internally, females of either *Calanus finmarchicus* or *Temora longicornis* were isolated and placed individually in 250 ml containers. The incubation chambers were fixed with net at the bottom to prevent cannibalism, mesh size 200 µm or 350 µm for *C. finmarchicus* or *T. longicornis* respectively. The chambers were then placed in containers, filled with seawater filtered through 100 µm. The cultivation containers were kept in temperature controlled (as close to ambient temperature as possible) and darkened place for 24 hours. At the end of incubation, seawater from individual bottles was sieved through 15 µm net and the eggs counted on a Petri dish under stereo microscope. Females were checked for their condition and noted if they were healthy and swimming. If the females were injured or dead their egg production was excluded from the results. At the end of the experiment the proportion of females who spawned was determined.
3.2.3 Gut fluorescence

From a net tow (see method from chapter 3.2.2, egg production) zooplankton was collected for gut fluorescence analysis. The sample was gently poured out of the cod end of the net, and collected on a net with 200 µm mesh size. Zooplankton was transferred from the net into bags (each sample divided into 4–6 bags) and quickly frozen with freezing spray (Electrolube, MCF Minimal Charging Freezer, 400 mL Aerosol) and stored in dry ice. The samples were kept frozen on dry ice while transported to the lab, where they were stored in -80°C freezer until analyzed.

Gut content of females of *C. finmarchicus* and *T. longicornis* were quantified by the end of each season. For each measurement of gut florescence a number of 3–6 animals were used for *C. finmarchicus* and 6–11 for *T. longicornis* for each replicate. As many replicates were made as the sample provided, 1–16 replicates each time.

Gut florescence was made by putting the animals in 5 ml of 90% acetone for 2 to 3 hours, which demolished the body wall of the animals and extracted the chlorophyll *a* from the phytoplankton in the gut. During samples preparation (15–30 min), direct light was reduced as possible and the samples kept cool. Gut fluorescence was quantified in fluorometer

Figure 3.1 Map of sampling stations in bay Breiðafjörður in West-Iceland. Samples were collected from 15th May to 31st August in 2008 and from 4th April to 28th September in 2009. The data from the two stations were combined for this study analysis. Map is redrawn from Gunnarsson 1991. The dotted line depicts the 50m depth and dashed line the 200m contour.
(Turner Designs 10-AU Fluorometer) and the fluorometer was calibrated using dilution series of chlorophyll a standard. Measurements were made before and after addition of 3 drops of 10% HCL-acid into the sample, for conversion of chlorophyll a into pheopigments. Concentration of chlorophyll a in the copepod guts were calculated according to Bämstedt et al. (2000).

3.2.4 Gut clearance rate and ingestion rate

Samples for gut clearance rate were collected on 3rd and 8th of June 2009 for *T. longicornis* and *C. finmarchicus*, respectively. Samples were collected as described for the gut fluorescence experiment. Animals were gently transferred into a 25 liter cooler, filled with GF/F filtered seawater at ambient temperature. Subsamples were taken at incubation time of 0, 5, 10, 15, 20, 30, 45, 60 and 90 min. Samples in triplicate were collected each time. The samples were prepared for gut fluorescence measurements as described above.

Gut clearance rates were furthermore calculated based on equation given by Bämstedt et al. (2000), assuming an exponential decrease in gut fluorescence over time: 

\[ G_t = G_0 \times e^{-k \times t} \]

where \( G_t \) is gut content at time \( t \) (ng chl a female), \( G_0 \) is the starting gut content and \( k \) is the gut clearance coefficient. Temperature used was from the day when the gut content samples were taken.

Ingestion rate (I) was estimated by the equation \( I = G \times K \) was used (Bämstedt et al. 2000), where \( G \) is a measured gut content of the animals and \( K \) is the calculated gut clearance coefficient calculated from the average temperature of meters 0 – 50 from the day of the sampling and equation from Dam and Peterson (1988), \( K = 0.0117 + 0.001794 \times T \), where \( T \) is temperature (°C) at the day of measurements. The ingestion rate was converted from chlorophyll a to carbon by ratio of 40 (Riemann et al. 1989, Geider et al. 1997, Gutierrez-Rodriguez et al. 2010).

3.2.5 Carbon requirements and secondary production

Carbon requirements were calculated based on values from the literature and observation from Breiðafjörður. Carbon content of eggs used was 0.23 µg C egg\(^{-1}\) for *C. finmarchicus* (Ohman and Runge 1994) and 0.0883 µg C egg\(^{-1}\) for *T. longicornis* (Dam and Lopes 2003).

Dry weight of females of *C. finmarchicus* has been estimated to be 196 µg, based on measurements from the west coast of Iceland (pers. conv. Ástþór Gislason). Female carbon specific-weight of *C. finmarchicus* was estimated based on 50% of dry weight for comparability to Gislason (2005), therefore 98 µg C f\(^{-1}\). For *T. longicornis* no measurements are available for carbon content of the species from Icelandic waters, therefore values from Dam and Lopes (2003) of 10.3 µg C f\(^{-1}\) were used. To calculate the weight-specific egg production, the daily egg production rate was converted into carbon and divided with carbon content of the females.

Secondary production of the population was calculated based on local measurements and literature values. The dry weight of the female abundance (in m\(^{-2}\)) was multiplied with the weight-specific egg production (Kiørboe and Nielsen 1994) and specific egg production rate
was assumed to be representative for juvenile specific growth (Berggreen et al. 1988). Carbon requirements of the females to fuel the egg production observed in this study was calculated by multiplying the secondary production with the specific growth rate, 33% for comparison with previous studies in the North Atlantic Ocean (Gislason 2005, Stenevik et al. 2007, Debes et al. 2008, Gislason 2008). To convert carbon requirements back to the need of individual females the carbon requirements were divided with the number of females.

### 3.2.6 Grazing impact

Potential grazing impact on phytoplankton to maintain egg production was calculated based on estimation of daily carbon requirements divided by integrated phytoplankton biomass, measured on the day of the experiment. The integrated phytoplankton biomass was converted to carbon based on carbon to chlorophyll \(a\) ratio of 40 (Riemann et al. 1989, Geider et al. 1997, Gutierrez-Rodriguez et al. 2010).

### 3.2.7 Statistical analyses

Statistical comparison of egg production and gut content of females of \(T.\ longicornis\) and \(C.\ finnarchicus\) were tested against the parameters years (2008 and 2009), temperature and chlorophyll \(a\) by generalized linear model (GLM) with Poisson distribution and a log-link function, using the R software package (version 2. 13. 1). Comparison of female abundance and environmental factors were first tested with Poisson distribution but the data was over dispersed and the results not used. Second, Quasi-Poisson distribution was tested with similar results. Thus, female abundance was tested against the environmental factors by linear model (LM) and the data transposed to natural logarithm plus one. The models tested for statistical comparison are shown in table 2.1.

Statistical comparison of female abundance and environmental factors among the two sampling stations revealed no significant difference between the locations. Therefore the data from the two stations were combined into one dataset. When both stations were sampled in the same week, an average value of the data between the two stations was used.

In all cases the full model and reduced model were compared by using chi-squared two-way ANOVA and the model with the best fit was chosen for statistical analysis.
3.3 Results

3.3.1 Hydrographic features

The mean temperature of the upper 50 m of the water column was similar both years, with maximum difference of 1.5°C between the two years, occurring in August. The temperature increased from a low in April (~2.8°C) to a maximum in August (~10–12°C) and started to decrease again in mid-September (Figure 3.2.A).

Salinity changed relatively little with depth or season (data not shown). The salinity ranged from 34.2–34.9 psu during the study period and limited stratification was observed (Pers. Com. Erla Björk Örnólfsdóttir).

The depth-integrated chlorophyll $a$ (0–20 meters) fluctuated through the summers in Breiðafjörður, with several peaks through the seasons. In 2008 there was one major peak, in end of May (135.7 mg chl $a$ m$^{-2}$), while the concentration fluctuated from 40–90 m chl $a$ m$^{-2}$ for the rest of the summer. In 2009, two major peaks were observed, in end of May (141.0 mg chl $a$ m$^{-2}$) and end of July (147.6 mg chl $a$ m$^{-2}$) (Figure 3.2.B).

3.3.2 Female abundance of the key species

Annual mean abundance of females of *Temora longicornis* was ~21,000 f m$^{-2}$ in 2008 and ~5,000 f m$^{-2}$ in 2009, where the female abundance was significant higher in 2008 than in 2009 ($p<0.05$). In the former year, the abundance of females started to increase in May to a maximum of ~80,000 f m$^{-2}$ in June and a second maximum of ~60,000 f m$^{-2}$ in July but decreased from then on. In the second year the female abundance was low until mid-May when the abundance started to increase and reached a maximum of ~62,000 f m$^{-2}$. At the end of June no females were detected in the fjord but a second maximum was observed by mid-July, of ~8,000 f m$^{-2}$ and from the end of July and through September, the abundance of females was low (> 2,000 f $^1$ m$^{-2}$) (Figure 3.3). There was no significant connection between the female abundance and environmental parameters.

Females of *Calanus finmarchicus* were ~6,000 f m$^{-2}$ on average in 2008 and ~2,000 f m$^{-2}$ in 2009 and the difference in abundance was however not significant (Table 3.2). In 2008 there were four maximum in *C. finmarchicus* abundance, ~9,000 f m$^{-2}$ in early July, 12,000 f m$^{-2}$ in mid-July and ~14,000 f m$^{-2}$ in mid-August and ~8,000 f m$^{-2}$ in beginning of September. In 2009 the females were negligible in April but the females started to increase in number in the beginning of May. In 2009 there were three maximums in *C. finmarchicus* abundance, in June ~6,000 f m$^{-2}$, in July of ~5,000 f m$^{-2}$ and in the beginning of September of ~8,000 f m$^{-2}$, followed by decrease in abundance. By the end of September female abundance had decreased and was negligible (Figure 3.3). The female abundance was in in negative correlation with chlorophyll $a$ concentration of the ocean.
Figure 3.2 Seasonal and annual variation in temperature and chlorophyll a concentration in Breiðafjörður. Samples were collected from 15th May to 31st August in 2008 and from 4th April to 28th September in 2009. A) Measured average temperature (°C) from depths 0–50 m. B) Integrated (0-20 m depth) chlorophyll a concentration (Chl a mg m$^{-2}$).
3.3.3 Feeding activity

Gut content of *T. longicornis* females was on average 1.69 ng chl a f\(^{-1}\) in 2008 and 3.07 ng chl a f\(^{-1}\) in 2009 whereas the annual difference was significant (p<0.05) (table 2.1). In 2008 the gut content of *T. longicornis* females ranged from 0.63 ng chl a f\(^{-1}\) to 4.35 ng chl a f\(^{-1}\) and was observed highest in the end of May. In 2009 the gut content ranged from 1.7 ng chl a f\(^{-1}\) to 8.01 ng chl a f\(^{-1}\) with highest values observed in September (Figure 3.4.A).

Gut content of *C. finmarchicus* females was on average 2.56 ng chl a f\(^{-1}\) in 2008 and 4.97 ng chl a f\(^{-1}\) in 2009 and the difference in amount was significant between the two years (p<0.05). In the former year the gut content of females ranged from 1.26 ng chl a f\(^{-1}\) to 8.31 ng chl a f\(^{-1}\) and was highest in end of May while values below 3 ng chl a f\(^{-1}\) were measured for the rest of the summer. In the latter year, the gut content of females ranged from 1.63 ng chl a f\(^{-1}\) to 9.76 ng chl a f\(^{-1}\), and was highest in mid-April although multiple peaks were observed through the summer (Figure 3.4.B). The gut content of females of *C. finmarchicus* was positively correlated with chlorophyll a concentration (p<0.05) and negatively correlated with temperature at the sampling day (Table 3.2).
Figure 3.3 Annual abundance of females (number m$^{-2}$) in summers 2008 and 2009. 
A) Temora longicornis and B) Calanus finmarchicus
3.3.4 Gut clearance rate

The gut clearance coefficient determined based on gut rate experiment was 0.009 min\(^{-1}\) (Figure 3.5). However, comparison with the gut clearance coefficient calculated from a model of Dam and Peterson (1988) was an order of magnitude higher, 0.098911 min\(^{-1}\), calculated for the ambient temperature.
5. Gut clearance rate measurements for Calanus finmarchicus at ambient temperatures, 7.33°C. Gut clearance coefficient was 0.009 min⁻¹. Diamonds represents measurements on gut content at each time.

3.3.5 Ingestion rate and carbon requirements

Average ingestion rate of *T. longicornis* was 11.1 µg C f⁻¹ d⁻¹ in 2008 and 18.2 µg C f⁻¹ d⁻¹ in 2009. In 2008, two maximum in ingestion rate were observed, one of 24.8 µg C f⁻¹ d⁻¹ in May, and the second of 12.3 µg C f⁻¹ d⁻¹ in July. In 2009, the ingestion rate increased from 8.9 µg C f⁻¹ d⁻¹ in mid-April to maximum of 21.8 µg C f⁻¹ d⁻¹ in end of June and decreased again thereafter. A second maximum in ingestion rate of *T. longicornis* was in September, of 59.6 µg C f⁻¹ d⁻¹ (Figure 3.6.A). Carbon requirements of *T. longicornis* were on average 1.4 µg C f⁻¹ d⁻¹ in 2008 and 14.0 µg C f⁻¹ d⁻¹ in 2009. The carbon requirements in 2008 were highest 3.6 µg C f⁻¹ d⁻¹ in June and decreased to 0 µg C f⁻¹ d⁻¹ in July. During 2009 the carbon requirements ranged between 11.1 to 16.7 µg C f⁻¹ d⁻¹ through the summer (Figure 3.6.A).

Ingestion rate of *C. finmarchicus* was on average 18.1 µg C f⁻¹ d⁻¹ in 2008 and in 2009 the average ingestion rate was 29.8 µg C f⁻¹ d⁻¹. Through the year 2008 the ingestion rate peaked at 47.2 µg C f⁻¹ d⁻¹ in May but ranged from 3.4 to 8.0 µg C f⁻¹ d⁻¹ for the rest of the summer. In 2009 the ingestion rate of *C. finmarchicus* oscillated through the summer with approximately monthly maximum. The maximum were the following: 28.4 µg C f⁻¹ d⁻¹ in April, 40.4 µg C f⁻¹ d⁻¹ in May, 63 µg C f⁻¹ d⁻¹ in June, 63.4 µg C f⁻¹ d⁻¹ in July, 52.1 µg C f⁻¹ d⁻¹ in August. Between the maximum the ingestion rate was below 23.6 µg C f⁻¹ d⁻¹ (Figure 3.6.B). Carbon requirements of *C. finmarchicus* were on average 23.2 µg C f⁻¹ d⁻¹ in 2008 and 29.0 µg C f⁻¹ d⁻¹ in 2009. The carbon requirements in 2008 were at one maximum in July, of 41.7 µg C f⁻¹ d⁻¹ while in 2009 the carbon requirements were sporadic at maximum through the summer, ranging from 9.5 µg C f⁻¹ d⁻¹ to 47.7 µg C f⁻¹ d⁻¹.
Figure 3.6 Ingestion rate and carbon requirements (µg C f$^{-1}$ d$^{-1}$) for egg production of females in 2008 and 2009. A) Temora longicornis and B) Calanus finmarchicus.
Table 3.1 General linear model (GLM) and linear model (LM) analysis between egg production, gut content and female abundance of *T. longicornis* and *C. finmarchicus* tested against environmental factors, location and time factor. Samples were collected in Breiðafjörður, West-Iceland, in summers of 2008 and 2009. The model setup of the statistical test, where the measured parameters were tested together. Each model was tested in full and reduced model and ANOVA analysis used to compare the two models. Numbers of measurements are seen within table. Table legend: LM = linear models, GLM = general linear models, # measurements = number of measurements, t0 = temperature of the sampling day, t1 – t3 temperature one to three weeks prior the sampling day, chl a = chlorophyll a concentration, egg = egg production rate, gut = gut content, female = female abundance.

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Table 3.2 General linear model (GLM) and linear model (LM) analysis between egg production, gut content and female abundance of *T. longicornis* and *C. finmarchicus* tested against environmental factors, location and time factor. Samples were collected in the fjord Breiðafjörður, West-Iceland, in summers of 2008 and 2009. The table displays the results from the statistical analysis of GLM and LM where the values represent the p-values from GLM or LM. Level of significance: *p<0.05*. Numbers of measurements are seen within the table. Figure legend: see Table 3.1.

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3.3.6 Fecundity

On average the population egg production rate of *T. longicornis* were 7.1 eggs f⁻¹ d⁻¹ in 2008 and 51.8 eggs f⁻¹ d⁻¹ in 2009. Egg production of *T. longicornis* was significantly higher in 2009 than in 2008 (p<0.05). In 2008 the egg production rate of the females varied from 0–46 eggs f⁻¹ d⁻¹ through the summer, with highest individual egg production detected in June followed by decline in production through July. In 2009 the egg production varied from 0–139 eggs f⁻¹ d⁻¹ and the highest egg production was detected in June (Figure 3.7.A). The proportion of spawning females of *T. longicornis* in 2008 was 92% in June and decreased through the summer and was 0% in July. In 2009 the percentage of spawning females was 90% in May while 100% of the females spawned until the end of the summer (Figure 3.8.A). Egg production of *T. longicornis* was negatively correlated with temperature at the sampling day and week prior the sampling (p<0.05) (Table 3.2).

Egg production rates of *C. finmarchicus* females was on average 27.9 eggs f⁻¹ d⁻¹ in 2008 and 42.3 eggs f⁻¹ d⁻¹ in 2009, where the annual difference in rate of egg production was not significant. In the former year the egg production of individual females ranged from 0–130 eggs f⁻¹ d⁻¹ with low production in June and highest average production of 59.8 eggs f⁻¹ d⁻¹, in July. In 2009 the egg production rates of individual females ranged from 0–150 eggs f⁻¹ d⁻¹. The production rate was on average 13.6 eggs f⁻¹ d⁻¹ in May, with a maximum of 58.8 eggs f⁻¹ d⁻¹ in June and a second maximum in August of 68.5 eggs f⁻¹ d⁻¹ (Figure 3.7.B). Spawning females of *C. finmarchicus* in 2008 were between 80–94% of all females and the proportion was highest in June. In 2009 the females who spawned were ~21% in May and the proportion of spawning females increased to 100% spawning of females in August by the end of the study period (Figure 3.8.B). Egg production rate of *C. finmarchicus* was positively correlated with the gut content of the females (p<0.05) (Table 3.2).
3.3.7 The population production and grazing

Weight-specific egg production of *T. longicornis* was on average 0.04 µg C µg C\(^{-1}\) d\(^{-1}\) in 2008 and 0.44 µg C µg C\(^{-1}\) d\(^{-1}\) in 2009. In 2008 the specific egg production was measured highest in June, 0.12 µg C µg C\(^{-1}\) d\(^{-1}\) and decreased to 0.01 µg C µg C\(^{-1}\) d\(^{-1}\) in July. In 2009 specific egg production was 0.36 µg C µg C\(^{-1}\) d\(^{-1}\) in May and increased to a maximum of 0.54, µg C µg C\(^{-1}\) d\(^{-1}\) in June. In July the specific egg production decreased again to 0.37 µg C µg C\(^{-1}\) d\(^{-1}\), and in August a second maximum was reached, 0.46 µg C µg C\(^{-1}\) d\(^{-1}\) (Figure 3.10.A).

Weight-specific egg production of *C. finmarchicus* was on average 0.08 µg C µg C\(^{-1}\) d\(^{-1}\) in 2008 and 0.1 µg C µg C\(^{-1}\) d\(^{-1}\) in 2009. The former year, the specific egg production was measured 0.01 µg C µg C\(^{-1}\) d\(^{-1}\) in June and increased until July when it reached a maximum of 0.14 µg C µg C\(^{-1}\) d\(^{-1}\). In August the specific egg production decreased again, to 0.07 µg C µg C\(^{-1}\) d\(^{-1}\). In the second year the initial weight-specific egg production was 0.03 µg C µg C\(^{-1}\) d\(^{-1}\) in May but reached a maximum in June, 0.14 µg C µg C\(^{-1}\) d\(^{-1}\). For the rest of June and through July the specific egg production ranged between 0.09 µg C µg C\(^{-1}\) d\(^{-1}\) and 0.1 µg C µg C\(^{-1}\) d\(^{-1}\). In August a second maximum was observed, 0.16 µg C µg C\(^{-1}\) d\(^{-1}\) (Figure 3.10.B).

The relative portion of egg production of the total production of *T. longicornis* was on average 10.4% in 2008 while in 2009 the egg production was 18.4% of the total production. In both years the highest proportion of egg production of total production of
Figure 3.8 Relative frequency of spawning females in egg production experiments in Breiðafjörður, during 2008 and 2009. A) Temora longicornis and B) Calanus finmarchicus.
the females was in early June (Figure 3.10.A). For females of *C. finmarchicus* the egg production of estimated total production was on average 13.8% in 2008 and 18.8% in 2009. In both years the highest relatively proportion of egg production of total production was in June and July (Figure 2.10.B).

The secondary production of the *T. longicornis* population was on average 19.8 mg C m$^{-2}$ d$^{-1}$ in 2008 and 42.2 mg C m$^{-2}$ d$^{-1}$ in 2009. In 2008, the secondary production was at a maximum in June, 49.4 mg C m$^{-2}$ d$^{-1}$ and decreased to 0 mg C m$^{-2}$ d$^{-1}$ in July. During 2009, the secondary production was 70.2 mg C m$^{-2}$ d$^{-1}$ in May, when first measured, and increased to 92.8 mg C m$^{-2}$ d$^{-1}$ in beginning of June. Two weeks later, the secondary production suddenly declined to 13.9 mg C m$^{-2}$ d$^{-1}$ and in the end of June a second maximum of 30.8 mg C m$^{-2}$ d$^{-1}$ was observed. By the end of July the secondary production was at minimum, 3.3 mg C m$^{-2}$ d$^{-1}$ (Figure 3.11.A).

Secondary production of *C. finmarchicus* females was on average 89.2 mg C m$^{-2}$ d$^{-1}$ in 2008 and 33.3 mg C m$^{-2}$ d$^{-1}$ in 2009. In 2008 a minimum in secondary production was in June 8.7 mg C m$^{-2}$ d$^{-1}$ but secondary production increased steadily thereafter through the summer, until a maximum was reached in August, 178.9 mg C m$^{-2}$ d$^{-1}$. In 2009 the secondary production was 4.0 mg C m$^{-2}$ d$^{-1}$ in May and increased to a maximum in the beginning of June, 85.4 mg C m$^{-2}$ d$^{-1}$ and was followed by decline to a minimum of 1.2 mg C m$^{-2}$ d$^{-1}$ by end of July (Figure 3.11.B).

The grazing rate of *T. longicornis* was on average 3.6% d$^{-1}$ of the phytoplankton biomass in both years 2008 and 2009. In 2008 the highest grazing rate of 10.2 % d$^{-1}$ was observed in the beginning of June, followed by a decline through the summer, to a minimum of 0 % d$^{-1}$ in July. In 2009 the grazing rate was at maximum in the beginning of June, 8.2 % d$^{-1}$ and decreased to a minimum of 0.1% d$^{-1}$ by the end of July (Figure 3.12.A).

Grazing rate of *C. finmarchicus* was on average 11.7 % d$^{-1}$ in 2008 and 4.8 % d$^{-1}$ in 2009. In 2008 the grazing rate increased from 1.2 % d$^{-1}$ in June to a maximum of 21.0 % d$^{-1}$ in August, while in 2009 the grazing rate increased from 1.4 % d$^{-1}$ in May to a maximum of 11.3 % d$^{-1}$ in June. A second maximum was in July, 8.62 % d$^{-1}$ and for the rest of the summer the grazing rate was below 1% d$^{-1}$ (Figure 3.12.B).
Figure 3.9 Weight-specific egg production of females in Breiðafjörður during 2008 and 2009. A) Temora longicornis and B) Calanus finmarchicus.
Figure 3.10 Percent contribution of egg production of the stocks total production in Breiðafjörður during 2008 and 2009. A) Temora longicornis and B) Calanus finnarchicus.
Figure 3.11 Secondary production of females in Breiðafjörður during 2008 and 2009. A) Temora longicornis and B) Calanus finmarchicus.
Figure 3.12 Grazing rate (% d⁻¹) of females of the total chlorophyll a measured in Breiðafjörður during 2008 and 2009. A) Temora longicornis and B) Calanus finmarchicus.
3.4 Discussion

3.4.1 Egg production rates

The study covered the entire egg production period of Temora longicornis and Calanus finmarchicus in Breiðafjörður in 2009 while in 2008 egg production might have started prior to the initiation of the sampling period. Egg production of Temora longicornis and Calanus finmarchicus were high through June and July in Breiðafjörður.

The percentage of spawning females of C. finmarchicus was similar to what previous studies have reported in the middle of the summer (58-79%), although in May the percentage of spawning females was lower (20-40%) (Jónasdóttir and Koski 2011). The egg production was thus most likely not fully started in the beginning of the summer and was at maximum in June-August. The proportion of spawning females of T. longicornis was similar to previous records in 2009 (58-100%) while in 2008 the first egg production experiment was in similar range and thereafter decreased sharply (Evjemo et al. 2008). The condition in June-August in Breiðafjörður seems therefore not to have been favorable for spawning of T. longicornis in 2008. Evjemo et al. (2008) discussed that present contents of docosahexaenoic acid (DHA, omega-3 fatty acid) in the food environment was one of the component affecting the rate of egg production for T. longicornis. DHA is rich in dinoflagellates and many smaller flagellates. Furthermore, egg production of T. longicornis has been shown not to correlate with food concentration (Evjemo et al., 2008). Jónasdóttir and Koski (2011) discussed that autotrophic dinoflagellates, flagellates and ciliates positively affect the egg production rate of C. finmarchicus. Thus, even though chlorophyll a concentration was high in Breiðafjörður during the low spawning, potentially other factors not measured in this study may have caused low egg production.

Feeding and fecundity of T. longicornis and C. finmarchicus has been shown to be correlated with maximum chlorophyll a concentration at times, whereas in other cases limited or no correlation has been detected (Kiørboe and Nielsen 1994, Niehoff et al. 1999, Campbell and Head 2000, Jónasdóttir et al. 2005, Stenevik et al. 2007). Thus, in some cases the egg production seems to be coupled with chlorophyll a concentration in the ocean, the quality of the food has been shown at times to be of more importance for the egg production and hatching (Jónasdóttir and Kiørboe 1996, Arendt et al. 2005). In Breiðafjörður the egg production of the two species, T. longicornis and C. finmarchicus were differently associated with chlorophyll a concentration.

Gut content and egg production of T. longicornis were not correlated with phytoplankton concentration (measured as chlorophyll a), which indicates that T. longicornis did not base its egg production solely on the phytoplankton standing stock. Additionally, the number and frequency of the measurements of the parameters; chlorophyll a, egg production and feeding rate may all have affected the lack of relationship between egg production rate and environmental factors. Due to low number of measurements the correlation between egg production rate and gut content of the females could not be determined. Within Breiðafjörður the egg production of T. longicornis was significantly lower in 2008 than in 2009. Despite the annual difference in egg production, the numbers for both years were
within range of records from other studies (Kiørboe and Nielsen 1994, Halsband and Hirche 2001, Dam and Lopes 2003, Devreker et al. 2005, Debes et al. 2008, Evjemo et al. 2008). Furthermore, these studies revealed that egg production of *T. longicornis* was related to food concentration. A couple of studies have revealed that diatom diet supported high egg production rates of *T. longicornis* (Dam and Lopes 2003, Arendt et al. 2005). Phytoplankton monitoring in Breiðafjörður in the years 2008 and 2009 revealed subtle peaks of diatoms in 2009 that were not apparent in 2008, therefore diatoms might have supported the higher egg production rate in 2009.

The gut content of *C. finmarchicus* in Breiðafjörður was significantly correlated with chlorophyll *a* concentration, while egg production rate was not. Egg production rates were though positively correlated with the gut content. Hirche (Hirche, 1996) gave account for the daily egg production to decrease sharply after 2 days of starvation at 0°C. Thus, in the 24h incubation of the females, the egg production was based on food they ingested approximately 1-2 days before the incubation. Jónasdóttir et al. (2005) discussed that when chlorophyll *a* is not limiting the egg production rate, a correlation between egg production rates and chlorophyll *a* concentration may not be detected. Thus, other factors than measured in this study might be affecting the egg production, such as dinoflagellates, flagellates and ciliates (Jónasdóttir and Koski 2011). Egg production of *C. finmarchicus* was not significantly different between the years which contrast the response which was observed with *T. longicornis*. The rate of egg production of both *C. finmarchicus* and *T. longicornis* in Breiðafjörður was within range of previous records of egg production observed. However, egg production in Breiðafjörður was high through the summer while egg production has been characterized by one or two peak in other areas (Harris et al. 2000, Runge et al. 2006, Gislason 2008, Dutz et al. 2012). Egg production rate of *C. finmarchicus* in Breiðafjörður was in no correlation with immediate temperature of the oceans which reflect the results of Jónasdóttir and Koski (2011) and Jónasdóttir (2008), where it was concluded that water temperature previously experienced by the copepods did not affect the egg production.

Within Breiðafjörður, maximum egg production of both *T. longicornis* and *C. finmarchicus* is later in the summer than observed elsewhere. For example the maximum is in early spring for *T. longicornis* in the North Sea, Eastern English Channel and in the Baltic Sea (Arendt et al. 2005, Devreker et al. 2005, Dutz et al. 2012), in April to May for *C. finmarchicus* in Greenland (Swalethorp et al. 2011) but in June for both species in the Faroe Islands water (Debes and Eliasen 2006). Furthermore, *C. finmarchicus* in offshore areas south of Iceland in May while on shelves areas in the south coast highest egg production observed have been observed in June (Gislason 2005). The high egg production through the summer in Breiðafjörður in both years and maximum during mid-summer might be caused by the unique ecosystem of Breiðafjörður, in which no stratification occurred during summer and constant mixing of the water column due to oceanic currents and wind effects.

### 3.4.2 Carbon demands

Ingestion rate and carbon requirements for *T. longicornis* were high in Breiðafjörður through both summers compared to observations from the White Sea (Martynova et al. 2011) and Long Island Sound, USA (Dam and Peterson 1991). In both years there was a
parallel pattern between the ingestion rate of the females and carbon requirements although the carbon requirements was approximately an order of magnitude lower in 2008. This indicates that T. longicornis based its egg production on the phytoplankton standing stock within Breiðafjörður in both years. The lack of correlation between chlorophyll a concentration and egg production rate of T. longicornis could be an indication of chlorophyll a as non-limited factor. Ingestion rate of C. finmarchicus within Breiðafjörður resembled the observation from the Irminger Sea (Gislason 2008) and from the Faroe Shelf (Jónasdóttir et al. 2008). In 2009 the ingestion rate in Breiðafjörður was double what was observed in 2008. The ingestion rate and carbon requirements were contrasting in 2008 while in 2009 they resembled each other, indicating that females of C. finmarchicus supported their egg production by other sources than phytoplankton. Non-chlorophyll containing particles, such as ciliates, have been shown to be a significant source of carbon to fuel the egg production of C. finmarchicus (Ohman and Runge 1994, Jónasdóttir et al. 2005). However, ciliates were not quantified in Breiðafjörður in 2008 and 2009. The secondary production of C. finmarchicus population in 2008 was more than double that observed in 2009, which was due to higher abundance of C. finmarchicus females in 2008 compared to 2009. These findings of female abundance as the main influence on the secondary production in Breiðafjörður are in harmony to what has been shown from C. finmarchicus in the North Sea (Jónasdóttir and Koski 2011) and Norwegian Sea (Niehoff et al. 1999).

Gut clearance rate was measured on a cruise on 8th of June in 2009. The observed gut clearance coefficient was 0.009 min⁻¹, which is an order of magnitude lower than calculated for C. finmarchicus females in The Faroe Islands, where Debes et al. (2008) observed gut passage time of 0.033 min⁻¹. It was concluded that due to low slope of gut clearance coefficient that the females had already cleared their gut prior to the initiation of the experiment. By calculating the gut clearance rate based on equation given by Dam and Peterson (1988) and the temperature of Breiðafjörður, a gut clearance rate of 0.099 min⁻¹ was estimated and used for these calculations (Debes et al. 2008). The estimates presented above are thus based on calculations but not the response rate of the species in Breiðafjörður. This may cause inaccuracy in the estimates and thus, the results should be taken cautiously.

The average secondary production of C. finmarchicus in Breiðafjörður (33.3-89.2 mg C m⁻² d⁻¹) was in the upper range of observations for C. finmarchicus production in the North-Atlantic (Gislason 2005, Jónasdóttir and Koski 2011, Swalethorp et al. 2011). Compared to published values of secondary production of small neritic species, the secondary production of T. longicornis in Breiðafjörður in the year 2008 was similar to former observation whereas in 2009 the production was twice as high in Breiðafjörður as former observations (Madsen et al. 2008, Koski et al. 2011).

T. longicornis and C. finmarchicus revealed different annually variability in secondary production within Breiðafjörður in 2008 and 2009. The secondary production of C. finmarchicus was high in Breiðafjörður in 2008 while in 2009 the female abundance was lower causing the population egg production to be being lower. However, the secondary production of T. longicornis was lower in 2008 than in 2009, where the female abundance was greater in 2009 than 2008. The measurements of this study were not comprehensive.
enough to address the question of the annual difference in secondary production observed in the two species. It has been pointed out that lipid reserves of *C. finmarchicus* from the year before can fulfill the energy requirements egg production (Jónasdóttir et al. 2008) but that *T. longicornis* is lacking lipid reserves (Mayzaud et al. 1992) and may therefore show immediate respond in egg production in relation to changes in food availability (Kreibich et al. 2008). Weather these factors or other unexplained factors played a role in Breiðafjörður remains to be determent.

Estimates of population egg production in the ecosystem of Breiðafjörður were based on average female abundance, percent spawning females and egg production of *Temora longicornis* and *Calanus finmarchicus*. The population egg production was dependent on female abundance and percent of spawning females more so than female fecundity. The secondary production of *T. longicornis* was high early in the summer and declined onward in both summers. Whereas the population egg production of *C. finmarchicus* increased steadily from June to August in 2008 while in 2009 the population production peaked in June and July. These contrasting patterns were mainly influenced by number of eggs and percentage of spawning females for *T. longicornis* in 2008 while in 2009 the egg production and percentage spawning females were the main contributing components to the secondary production. For *C. finmarchicus* the female abundance was the controlling factor of the secondary production estimates. These estimates indicate that biological responses of *T. longicornis* were in close connection to the ecological conditions of the two years whereas *C. finmarchicus* did not respond as greatly to the environmental conditions.

The abundance of both *T. longicornis* and *C. finmarchicus* females were significantly higher in 2008 than in 2009, as well as the total abundance of the species (Sigurðardóttir unpublished). In contrast, the rate of egg production of *T. longicornis* was significantly higher in 2009 than in 2008, whereas the rate of egg production of *C. finmarchicus* was not significantly different between the two summers. Thus, the high female abundance of *T. longicornis* in 2008 with lower percentage of spawning resulted in a similar secondary production of the species between the years. Planktonic animals must deal with great temporal and sporatic variations in the environment, which can be both extreme and extensive as well as not repreasentative between years (Mackas et al. 2012). This variation in the environment can causes annual variations in abundance, species composition as well as secondary production of copepods within the ocean.

### 3.4.3 Conclusion

In Breiðafjörður the oceanic environment is spatially and annually variable, which is reflected in copepods abundance and species composition (Sigurðardóttir unpublished). In this context it is interesting to investigate further how egg production is varies between the two key copepod species in Breiðafjörður. In this study a spatial variability was excluded in the analysis and the main focus was on seasonal and annual variability. Further estimations on the secondary production in annual and spatial context within Breiðafjörður are of importance to understand the dynamics of energy flux through the tropical levels of the food chain (Avila et al. 2012).
The dynamic ecosystem of Breiðafjörður makes the location of great interest for studies on the response rate of copepods to various environmental parameters, and the effect on copepod phenology, their community composition and fate. In times when global warming has great impacts to the oceanic environment (Richardson and Schoeman 2004, Hays et al. 2005, Sommer and Lewandowska 2011, Mackas et al. 2012) and the interest in understanding the consequences of warming oceans is growing. The easily accessible ecosystem Breiðafjörður could be a case study area for copepod response to frequent and unpredictable pulses in environmental conditions.

Further studies on the various copepod communities within Breiðafjörður would be of great interest to determine the underlying component affecting the various productions of the two species temporally and spatially within the bay. In the unpredictable environment of Breiðafjörður, a frequency of sampling such as 10 days interval as conducted in this study only gives a fragmentary image of the factors influencing the secondary production of the bay. A study based on mesocosms where the underlying components of Breiðafjörður would be tested both separately and combined could provide more detailed information on the controlling factors of the secondary production of the bay.

4 Conclusions

Breiðafjörður is an area of great interest as model environment for zooplankton research. The environment is annually and spatially variable, where oceanic currents and wind effects cause limited or lack of stratification within the fjord, and thus, support pulses in environmental conditions. The study area provides therefore an insight into the dimensions that copepods can tolerate in the upper ocean. Furthermore, the study area is small and accessible.

In this study the main emphasis was on annual and seasonal variations of abundance, species composition, fecundity and feeding of the most abundant copepods of Breiðafjörður. For clear focus on the temporal variation in abundance, feeding and fecundity, the two stations were combined and thus, a spatial variability excluded from the analysis. Although statistical tests (LM and GLM) revealed that no significant difference was between the stations in abundance in most cases (all except for abundance of *Pseudocalanus* sp.) the timing of events varied. However, the combination of the two stations was done to get more detailed image of the annual and seasonal variation.

In Breiðafjörður it would be interesting to further analyze the variability within the copepod community as well as the secondary production to determine the factors affecting the variability. These factors could be temperature, mixing of the water column and currents, which cause variation in nutrient concentration and availability, phytoplankton standing stock (in both magnitude and species composition) and thus the copepod community and secondary production. A mesocosm study where these underlying components of Breiðafjörður would be tested, both individually and mixed, could provide an detailed information on the factors which control the variability within the bay, both in terms of copepod community as well as the secondary production.
5 References


Astthorsson, O. S. and A. Gislason. 1999. Inter-annual variation in abundance and development of *Calanus finmarchicus* in Faxaflói, West-Iceland. Rit Fiskideildar **16**:131-140.


Geider, R. J., H. L. MacIntyre, and T. M. Kana. 1997. Dynamic model of phytoplankton growth and acclimation: Responses of the balanced growth rate and the chlorophyll


Martynova, D. M., N. A. Kazus, U. V. Bathmann, M. Graeve, and A. A. Sukhotin. 2011. Seasonal abundance and feeding patterns of copepods Temora longicornis,
Centropages hamatus and Acartia spp. in the White Sea (66 degrees N). Polar Biology 34:1175-1195.


