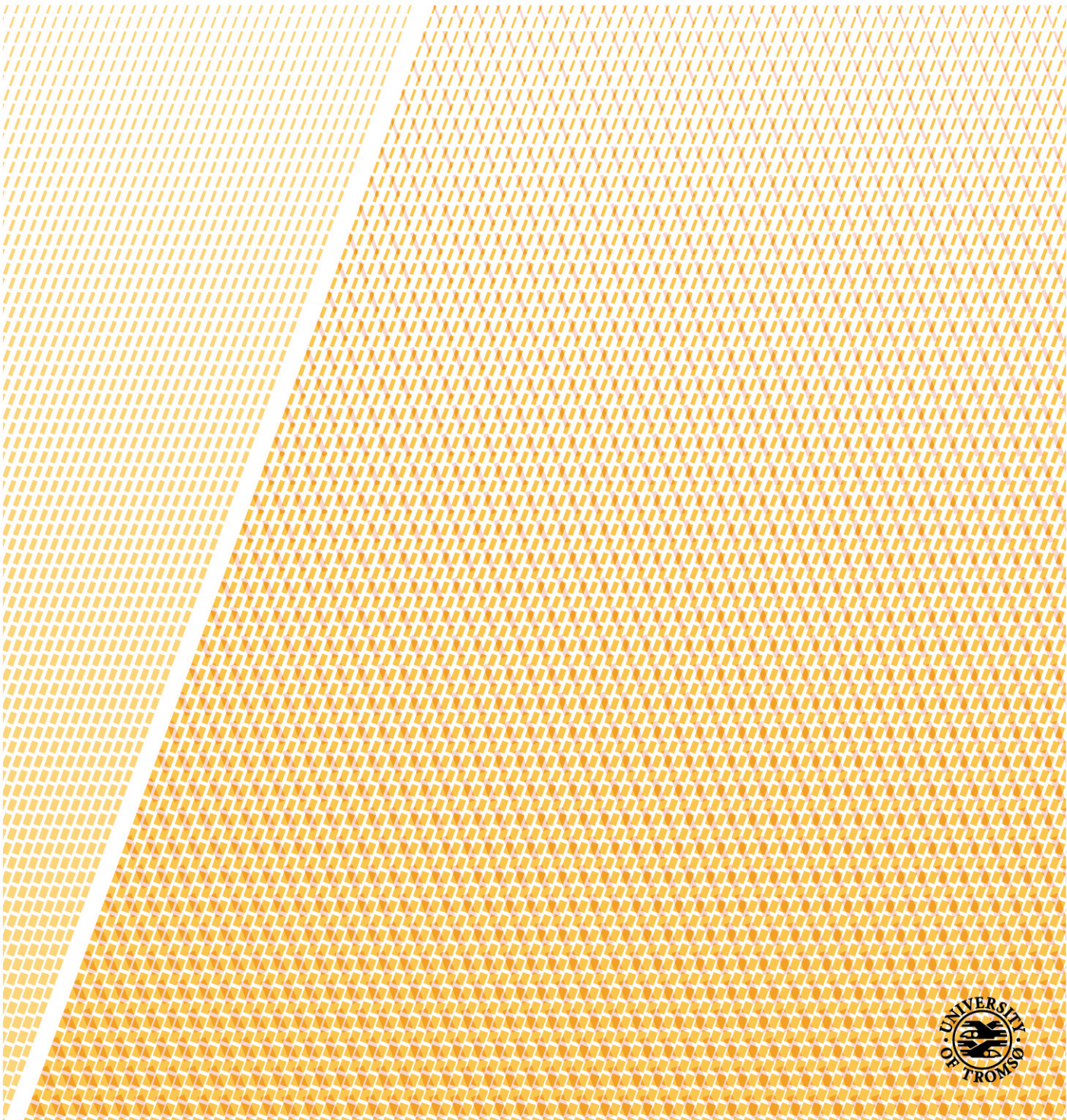# *Calanus glacialis* and *C. finmarchicus* in a warming Arctic

Implications of increasing temperature at the individual and population level

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Ulrike Grote
A dissertation for the degree of Philosophiae Doctor – November 2016

Calanus glacialis and *C. finmarchicus* in a warming Arctic

Implications of increasing temperature at the individual and population level

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To my parents
For making the ocean with everything in it
the most mysterious and wonderful place

CONTENTS

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SUMMARY

The Arctic marine ecosystems are strongly affected by climate change, experiencing substantial warming resulting in changes in the cryosphere and hydrography. The calanoid copepods *Calanus glacialis* and *C. finmarchicus* are key species of different pelagic food webs at high latitudes. They have similar morphologies, but can differ in size, geographical distribution and life history. Both species are well adapted to the short feeding season by synthesising and storing lipids making them valuable prey species. Temperature has a fundamental control over physiological processes of especially ectotherms, such as copepods, due to its influence on biochemical reaction rates and enzyme activity.

The distribution and success of a species depend on its ability to survive, grow, and reproduce under variable environmental conditions. One main objective of this thesis was to investigate physiological processes affecting growth and reproduction, such as feeding, egestion, respiration, and egg production rates of especially *C. glacialis* (copepodite stages V and adult females) in response to increasing temperature (0-10 °C) and to investigate and discuss the potential metabolic balance indicated by these processes. The other main objective of this thesis was to investigate the effect of increasing temperature at the population level of *C. glacialis* and *C. finmarchicus* at two different locations for each species, characteristic for their currently known biogeographical extent in the Barents Sea region, using an ecosystem model. The experimentally identified thermal responses in feeding and respiration were implemented into the coupled physical-biological SINMOD model system, to improve the representation of the mesozooplankton dynamics in the model.

While *C. glacialis* ingestion rates increased linearly with temperature in one experiment (Paper I), they reached a temperature optimum at 2.5 °C, decreasing again at higher temperatures in another experiment (Paper II), indicating plasticity in thermal responses, likely due to local adaptation. Similar to the ingestion rates, faecal pellet production of *C. glacialis* increased linearly with increasing temperature, but the increase was more pronounced than for the feeding response. Respiration rates of *C. glacialis* increased with temperature until a thermal optimum at 6 °C (Paper II). Egg production rates of *C. finmarchicus* increased linearly within the investigated temperature range, while egg production rates of *C. glacialis* followed an unimodal pattern with increasing temperature, with a thermal optimum at 2.5-5 °C (Paper III).

The metabolic balance of an organism and thus the energy available for allocation to growth and reproduction depends on the energetic outcome of processes governing metabolic gains, such as ingestion and assimilation efficiency, and metabolic losses, such as respiration, excretion and egestion. Comparing the Q_{10} values of ingestion, egestion and respiration rates of *C. glacialis* indicates that the physiological processes connected to metabolic losses have a higher thermal sensitivity than those connected to metabolic gains, resulting in relatively less energy being available for growth and reproduction at warmer temperatures (Paper I). A direct comparison of carbon specific ingestion and respiration rates of *C. glacialis* indicates a metabolic mismatch at temperatures above 5-6 °C, potentially resulting in negative effects on growth and survival (Paper II). Egg production rates reflect to some degree the metabolic balance of copepods. At temperatures above 5 °C, egg production rates decreased, indicating higher thermal sensitivity in processes governing metabolic losses, as opposed to processes governing metabolic gains (Paper III).

The simulated response of *C. glacialis* and *C. finmarchicus* populations with increasing temperature suggests that *C. finmarchicus* biomass and net production will increase in the southern Barents Sea (Paper IV). *C. glacialis* biomass and net production will most likely increase in the northern Barents Sea up to seawater temperatures of 5-6 °C. Further warming will very likely reduce *C. glacialis* biomass and net production due to the metabolic mismatch negatively affecting growth (Paper II and IV). While physiological responses to increasing temperature play an important role for both *Calanus* species, changes in food availability due to nutrient limitation will have more pronounced effects on population biomass and productivity, suppressing the potentially positive effects of initially increasing temperatures. A change from a system dominated by large, lipid-rich *C. glacialis* to relatively smaller, less lipid-rich *C. finmarchicus* or *C. glacialis* is likely to have a negative impact on the energy transfer in Arctic marine ecosystems.

LIST OF PAPERS

This thesis is based on the following papers, which are referred to in the text by their Roman numbers.

I **Grote U.**, Pasternak A., Arashkevich E., Halvorsen E., Nikishina A. (2015) Thermal response of ingestion and egestion rates in the Arctic copepod *Calanus glacialis* and possible metabolic consequences in a warming ocean. Polar Biology 38: 1025-1033

II * Alcaraz M., Felipe J., **Grote U.**, Arashkevich E., Nikishina A. (2014) Life in a warming ocean: thermal thresholds and metabolic balance of arctic zooplankton. Journal of Plankton Research 36(1): 3-10

III Pasternak A.F., Arashkevich E.G., **Grote U.**, Nikishina A.B., Solovyev K.A. (2013) Different effects of increased water temperature on egg production of *Calanus finmarchicus* and *C. glacialis*. Oceanology 53(5): 547-553

IV **Grote U.**, Eisenhauer L. Modelling population level responses of *Calanus glacialis* and *C. finmarchicus* under different climate warming regimes in the Barents Sea area. Manuscript

* **Paper II** is not a traditional research paper but a format called 'Horizons' in the Journal of Plankton Research. The paper is meant as a topical and provocative review, additionally presenting a case study. It contributes to this thesis only with this case study of the thermal feeding and respiration response and the resulting discussion regarding the metabolic balance of *C. glacialis*.

1.1   ARCTIC MARINE ECOSYSTEMS AND CLIMATE CHANGE

Due to their location at high latitudes, Arctic seas are strongly influenced by highly seasonal changes in incoming solar radiation, with the polar night during winter and midnight sun during summer, resulting in generally low water temperatures and the (seasonal) formation of sea ice (Fig. 1). Sea ice shortens the already restricted photoperiod by limiting the amount of photosynthetically active radiation (PAR) that is penetrating into the water column. Sea ice algae start growing under the ice at low light levels already as early as March, depending on ice thickness, and continue to grow until the ice melts (Hegseth 1998). The freshwater release due to sea ice melting in spring and summer leads to strong water column stratification, which restricts the replenishment of nutrients to the upper mixed water layer. A short and intense phytoplankton bloom follows the ice break up and the increasing light intensity in spring. The relatively short and variable period of primary production in Arctic marine ecosystems is nevertheless characterized by high biological activity.

The Arctic regions, both terrestrial and marine, are experiencing substantial warming since the 1950s, very likely due to anthropogenic forces (Bindoff et al. 2013). Arctic air surface temperatures are increasing at rates two to four times higher than the global rate, depending on the observed time interval (Bekryaev et al. 2010; Masson-Delmotte et al. 2013). Sea surface temperatures and Atlantic Water core temperature in the Arctic Ocean and its marginal seas have increased as well during the last decades (Polyakov et al. 2012; Polyakov et al. 2013; Hartmann et al. 2013). Increasing air and sea surface temperatures have already altered the Arctic cryosphere. The annual Arctic sea ice extent has decreased by 3.5-4.1 % per decade (1979-2012) with the most rapid decline in summer and autumn (Vaughan et al. 2013). Perennial and multi-year ice extents have decreased at even higher rates (Comiso 2012) and winter sea ice thickness has decreased accordingly (Kwok 2009; Wadhams et al. 2011; Laxon et al. 2013). Glaciers are shrinking and the Greenland ice sheet is losing ice at an accelerated rate since 1992 (Vaughan et al. 2013, and references therein). Additionally, the snow cover extent in the Northern hemisphere has decreased especially in spring (Brown and Robinson 2011).
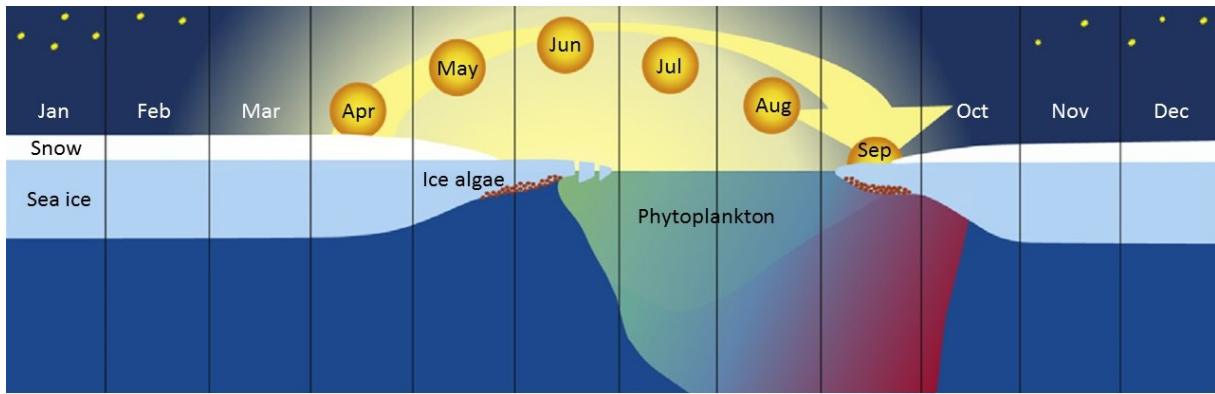
Fig. 1 Seasonal cycle of ice-covered Arctic marine ecosystems illustrating the change in incoming solar radiation, sea ice formation and melting, and ice algae and phytoplankton blooms. Figure modified from Wassmann (2011).

All of these changes are likely to contribute to more pronounced warming through so the called Arctic amplification, meaning that changes in ice, snow and sea surface albedo, cloud cover and water vapour will amplify the observed warming, affecting the climate of the Arctic region and probably beyond and will continue to do so (Serreze and Barry 2011, and references therein). Due to the Arctic amplification the Arctic regions are expected to exceed mean global warming by a factor of 2.2 to 2.4 (+2.2 to +8.3 °C, depending on the forcing scenario implemented by the International Panel of Climate Change) by the end of the 21st century compared to 1986-2005 (Collins et al. 2013).

1.2 CALANOID COPEPODS: ARCTIC KEY SPECIES

Copepods of the genus *Calanus* are well-adapted to the strong seasonality of the Arctic marine environment. They are key species of the pelagic food web at high latitudes, contributing significantly to the total zooplankton biomass and representing an important link between phytoplankton and organisms at higher trophic levels, such as fish, seabirds and marine mammals (Conover 1988; Mumm et al. 1998; Søreide et al. 2008; Falk-Petersen et al. 2009). The genus *Calanus* is mainly represented by three species in the Arctic and sub-Arctic areas: *Calanus hyperboreus*, *C. glacialis* and *C. finmarchicus*. They are similar in morphology, but can differ in size, geographical distribution and life history. The latter two species are the target organisms of this thesis (Fig. 2).

The relatively large *C. glacialis* (2.8-4.2 mm adult female prosome length) is a true Arctic species, with its main distribution in the shallow Arctic shelf seas (Jaschnov 1970; Conover 1988; Kosobokova 1998), where it is an important food source for seabirds like little auks (*Alle alle*) (Weslawski et al. 1994; Karnovsky et al. 2003; Steen et al. 2007), fish like polar cod (*Boreogadus saida*) (Hop and Gjøsæter 2013), and bowhead whales (*Baleana mysticetus*) (Pomerleau et al. 2012). The smaller *C. finmarchicus* (1.9-3.3 mm) has its centre of distribution in the North Atlantic but may be expatriated with the currents into the central Arctic Ocean (Jaschnov 1970; Hirche 1991; Planque et al. 1997; Hirche and Kosobokova 2007). *C. finmarchicus* is an important food source for a number of commercial and non-commercial fish species, such as Norwegian spring-spawning herring (*Clupea harengus*) (Dalpadado et al. 2000), Atlantic mackerel (*Scomberus scomberus*) (Mehl and Westgård 1983), capelin (*Mallotus villosus*) (Dalpadado and Mowbray 2013), and Atlantic cod (*Gadus morhua*) (Helle and Pennington 1999). The distribution of the two *Calanus* species overlaps where Atlantic and Arctic Water masses meet, such as the Barents Sea (Falk-Petersen et al. 1999).

One main adaptation of these *Calanus* species to the short feeding season is the ability to synthetize and store energy rich lipids (Conover 1988; Lee et al. 2006; Falk-Petersen et al. 2009). However, *C. finmarchicus* usually contains less lipids than *C. glacialis* (Falk-Petersen et al. 2009). Another important adaptation of *Calanus* spp. to the strong seasonality in the Arctic is seasonal vertical migration. The life cycle of calanoid copepods consists of six naupliar stages (NI-NVI) and six copepodite stages (CI-CVI/adult stage) and *Calanus* spp. develop through the
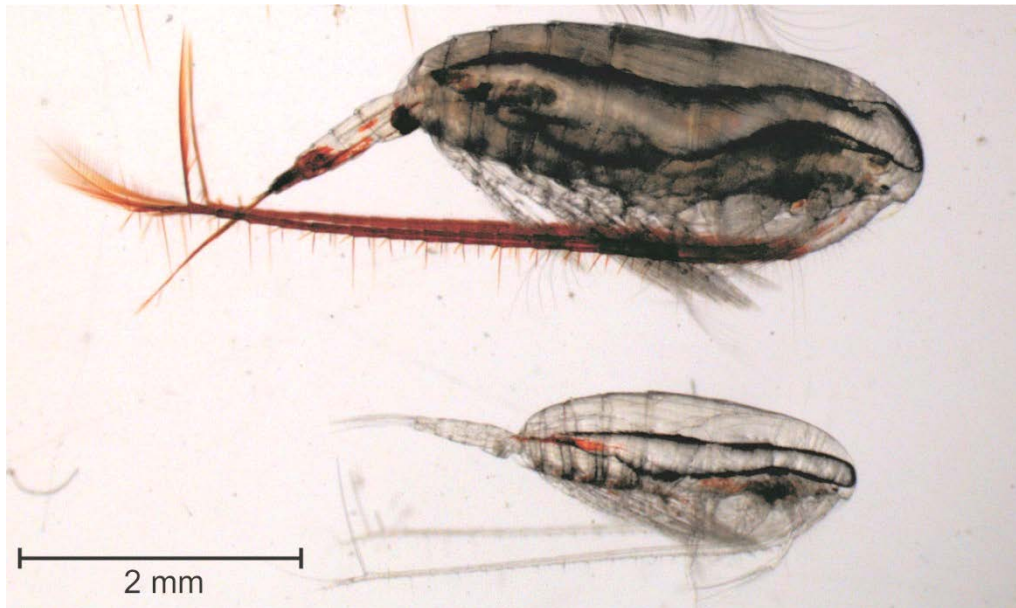
Fig. 2 *Calanus glacialis* adult female (top) and *C. finmarchicus* adult female (bottom). Picture: Malin Daase

different stages mainly during spring/summer. The late lipid-rich copepodid stages of *Calanus* spp. (CIII-CV) then descend to deep waters in late summer/autumn to overwinter in a state of dormancy. In the northern Barents Sea the main overwintering stages of *C. glacialis* are CIV and CV, resulting in a 2-year life cycle (Conover 1988; Arnkværn et al. 2005).

C. finmarchicus on the other hand has a 1-year life cycle in its northern area of distribution, with CV as the main overwintering stage (Falk-Petersen et al. 1999; Falk-Petersen et al. 2009). *C. finmarchicus* spawns during or just after the phytoplankton bloom peak and depends on external food supply to initiate and maintain spawning (e.g. Madsen et al. 2008; Swalethorp et al. 2011; Kjellerup et al. 2012). In contrast, *C. glacialis* spawns prior or during the spring bloom, with internal lipids and/or ice algae fuelling the maturation of gonads and egg production, while peak egg production rates often coincide with high chlorophyll *a* concentrations later in the season (e.g. Hirche and Bohrer 1987; Kosobokova 1998; Niehoff et al. 2002; Søreide et al. 2010). In seasonal ice covered seas *C. glacialis* has the advantage of being able to start reproduction prior to the onset of the phytoplankton bloom and will thus have a head-start to *C. finmarchiucs* who needs the energy supplied by the phytoplankton bloom to fuel maturation and reproduction (Kjellerup et al. 2012*)*.
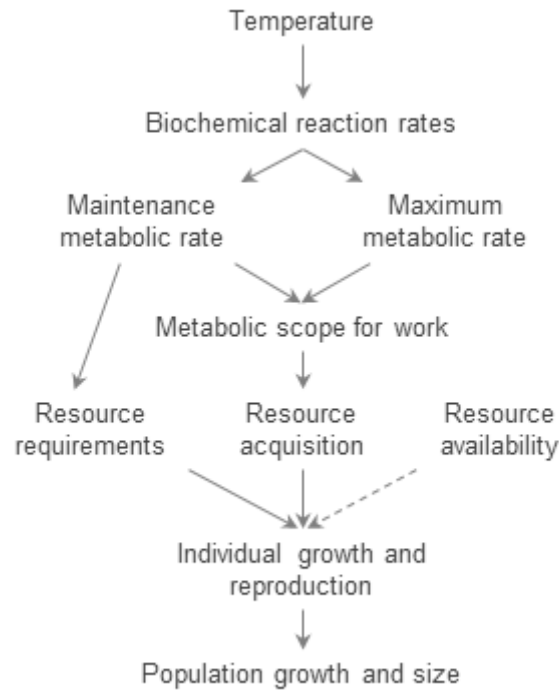
Fig. 3 Pathway by which (body) temperature influences the ecology of ectothermic organisms and populations. Adapted from Kordas et al. (2011) with permission from Elsevier.

1.3   THE BIOLOGICAL IMPORTANCE OF TEMPERATURE

Temperature not only shapes the Arctic environment physically but also biologically, since both, chemical and biochemical reaction rates depend on temperature. The importance of temperature for biological processes in ectotherms (organisms in which internal physiological sources of heat are of relatively small or quite negligible importance in controlling body temperature) is visualized in Fig. 3. Enzyme-catalysed biochemical reactions typically increase with temperature to a certain point (temperature optimum) after which they sharply decrease again (Angilletta 2009), a so called unimodal thermal response (Fig. 4). As enzymatic reactions are the basis of biological rates, these often express a similar relationship with temperature. Both, the maintenance metabolic rate (also called resting or basal metabolic rate, the rate at which an organism must expend energy to stay alive and healthy, e.g. respiration), and the maximum metabolic rate (the rate at which an organism can expend energy, e.g. during activity) depend on temperature. Kordas et al. (2011) named the difference between the maximum metabolic rate and the maintenance metabolic rate the metabolic scope for work, which determines the rate at which an organism can acquire resources, given that the resources are not limited. As individual growth rates depend on the energy available for biosynthesis (non-maintenance functions), they often display a unimodal relationship with temperature as well
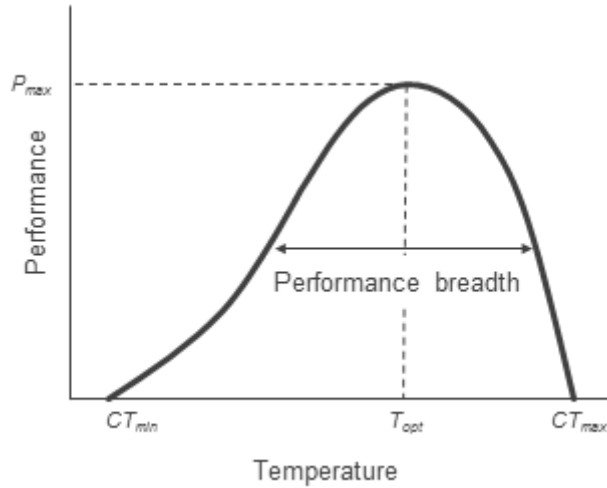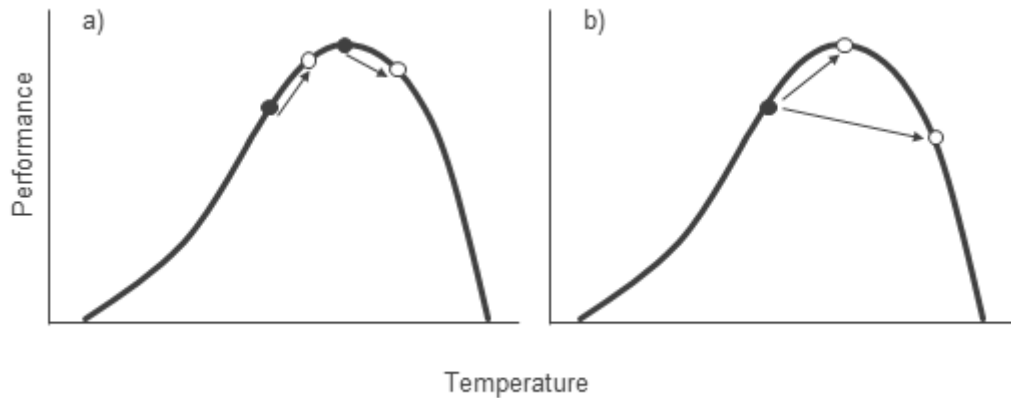
Fig. 4 Hypothetical thermal performance curve showing the temperature optimum (T_{opt}), performance breadth, critical thermal minimum (CT_{min}), critical thermal maximum (CT_{max}), and the maximal performance (P_{max}). Adapted from Huey and Stevenson (1979)

(Huey and Stevenson 1979; Angilletta 2009). Faster individual growth rates in combination with faster development rates due to increased temperature in turn reduce generation time, which has important consequences for population growth (Huey and Berrigan 2001) and abundance. Resource availability plays a crucial role and may ultimately affect individual performance and population dynamics in addition.

Theoretically, the sensitivity of an organism to rising temperatures can be assessed by using thermal performance curves (Fig. 4), which describe the variation in fitness-related traits across a range of temperature (Huey and Stevenson 1979; Ohlberger 2013). Common measures of organismal performance include locomotion, feeding/assimilation, growth, development, reproduction, and survivorship (Angilletta 2009). Generally, the thermal response can be characterized by several parameters (Fig. 4): 1) the thermal optimum (T_{opt}); 2) the performance or thermal breadth; 3) the thermal limits: the critical thermal minimum (CT_{min}) and the critical thermal maximum (CT_{max}); 4) and the maximal performance (P_{max}).

The effect of increasing temperatures on an organism's performance therefore depends on the organism's temperature optimum relative to the experienced environmental temperature and the magnitude of temperature increase (Ohlberger 2013). Increasing temperatures are expected to increase the performance of ectothermic organisms currently experiencing temperatures

Fig. 5 Hypothetical thermal performance curves illustrating the possible effects of climate change on performance of ectothermic organisms: a) increasing temperatures are expected to increase performance of organisms currently experiencing temperatures below the thermal optimum, whereas performance is expected to decrease for those currently experiencing temperatures at or above their thermal optimum; b) a moderate increase in temperature may increase performance, whereas a more severe temperature increase may decrease performance (in the absence of adaptation). Modified from Ohlberger (2013) with permission from John Wiley and Sons

below their thermal optimum (e.g. *C. finmarchicus* at its northern border of distribution), but decrease performance of those currently experiencing approximately optimal temperatures (e.g. *C. glacialis* in the northern Barents Sea; Fig. 5a). While moderate increases in temperature may increase organismal performance, severe temperature increases may decrease the performance of ectothermic organisms (Fig. 5b).

1.4   *CALANUS* AND TEMPERATURE

As key species of their respective food webs, both *Calanus* species have received some scientific attention regarding the effect of temperature on their abundance and biomass distribution, physiology, and life history traits. An overview of peer-reviewed publications is provided in Table 1, where relationships between temperature and 1) distribution, 2) survival/mortality, 3) growth and development, 4) feeding and faecal pellet production, 5) respiration, and 6) reproduction were investigated (mainly experimentally).

Table 1 Peer-reviewed literature investigating the effect of temperature on different parameters of *Calanus glacialis* and *C. finmarchicus*

Species	Objective	Temperature (°C)	Effect	Reference
C. finmarchicus	Abundance		No clear effect	Tande et al. (2000)
C. glacialis *C. finmarchicus*	Abundance		Decrease with temperature (<500 m) Increase with temperature	Daase et al. (2007)
C. finmarchicus	Abundance		Decrease with surface temperature	Kane (2007)
C. glacialis *C. finmarchicus*	Abundance and Biomass		Different effects in different years	Dvoretsky and Dvoretsky (2011)
C. finmarchicus	Probability of occurrence		Highest probability at 4.5-8.5 °C	Reygondeau and Beaugrand (2011)
C. glacialis *C. finmarchicus*	Biomass		Non-linear, threshold at 6 °C Linear increase	Carstensen et al. (2012)
C. finmarchicus	Long-term Survival (2-4 weeks)	3, 6, 9	Lowest mortality at 3 °C	Clarke and Bonnet (1939)
C. glacialis *C. finmarchicus*	Acute mortality (24 hours)	-1.8-24	50 % mortality at ~18 °C 50 % mortality at ~21 °C	Hirche (1987)
C. finmarchicus	Daily mortality rates (~40 days)	0.5, 3, 6	Highest mortality at 0.5 °C	Tande (1988a)
C. finmarchicus	Mortality	4, 8, 12	Higher mortality at 12 °C	Campbell et al. (2001)
C. glacialis *C. finmarchicus*	Daily mortality rates (~40 days)	0, 5, 10	Increasing with temperature	Grenvald et al. (2013)

Table 1 continued

Species	Objective	Temperature (°C)	Effect	Reference
C. glacialis *C. finmarchicus*	Development	0-10	Equiproportional	Corkett et al. (1986)
C. glacialis	Development	0-11	Equiproportional	McLaren et al. (1988)
C. finmarchicus	Growth Development	0.5, 3, 6	Increasing Not equiproportional	Tande (1988a)
C. finmarchicus	Growth Development	4, 8, 12	Increasing Equiproportional, not isochronal	Campbell et al. (2001)
C. glacialis *C. finmarchicus*	Early development	0, 5, 10	Decreasing with increasing temperature	Grenvald et al. (2013)
C. glacialis *C. finmarchicus*	Early development	0, 2.5, 5, 7.5, 10	Equiproportional Equiproportional	Jung-Madsen and Nielsen (2015)
C. glacialis *C. finmarchicus*	Egg development	0, 2.5, 5, 7.5, 10	Decreasing with increasing temperature	Weydmann et al. (2015)
C. finmarchicus	Clearance rates	2, 8, 15, 22.5	Unimodal response	Anraku (1964)
C. glacialis *C. finmarchicus*	(Specific) Faecal pellet production	0, 2.5, 5, 7.5, 10	Linear increase until 7.5 °C Linear increase until 10 °C	Kjellerup et al. (2012)
C. finmarchicus	Clearance rates	1-21	Unimodal response	Møller et al. (2012)
C. glacialis *C. finmarchicus*	Faecal pellet production	0, 5, 10, 15	Unimodal response Increase until 10 °C	Smolina et al. (2015)

Table 1 continued

Species	Objective	Temperature (°C)	Effect	Reference
C. finmarchicus	Respiration	5-17	Linear increase	Clarke and Bonnet (1939)
C. finmarchicus	Respiration	0, 5, 10, 15, 20	Linear increase	Marshall and Orr (1958)
C. finmarchicus	Respiration	2, 8, 15, 22.5	Increase until 15 °C	Anraku (1964)
C. glacialis *C. finmarchicus*	Respiration	0-18	Increase until 10 °C Linear increase	Hirche (1987)
C. glacialis	Respiration	-1.7-10	Increase from 5 °C	Tande (1988b)
C. glacialis	Respiration	-0.5, 3.5	No change	Ikeda and Skjoldal (1989)
C. finmarchicus	Diapause respiration	3.6-9.7	Linear increase	Saumweber and Durbin (2006)
C. finmarchicus	Daily egg production	5.3-13.5	Linear increase	Runge (1985)
C. finmarchicus	Daily egg production	-1.5-8	Linear increase	Hirche et al. (1997)
C. finmarchicus	Daily egg production	4, 8, 12	Lowest at 8 °C	Campbell et al. (2001)
C. glacialis	Egg production	-1.5, 2, 5, 8	Linear increase	Hirche and Kosobokova (2007)
C. glacialis *C. finmarchicus*	Egg production	0, 2.5, 5, 7.5, 10	Linear increase Linear increase	Kjellerup et al. (2012)
C. finmarchicus	Egg hatching success	6-26	Decrease from 19 °C	Preziosi and Runge (2014)
C. glacialis *C. finmarchicus*	Egg hatching success	0, 2.5, 5, 7.5, 10	No effect	Jung-Madsen and Nielsen (2015)
C. glacialis *C. finmarchicus*	Egg hatching success	0, 2.5, 5, 7.5, 10	No effect	Weydmann et al. (2015)

Even though the body of literature is relatively large, much less information is available for *C. glacialis* compared to *C. finmarchicus*. Prior to 2009, when this PhD project started, relatively little information was available about the effect of increasing temperature on respiration and egg production of *C. glacialis*, while no information was available on its effect on feeding (Table 1). While in recent years a number of studies has been performed, especially on the effect of temperature on reproductive traits, there is still a lack in investigations regarding its effect on feeding.

1.4.1 *Distribution*

Several studies have investigated if temperature, together with other environmental variables such as salinity, depth and sea ice concentration could explain the abundance and/or biomass distribution of *C. glacialis* and *C. finmarchicus* (Tande et al. 2000; Daase et al. 2007; Kane 2007; Dvoretsky and Dvoretsky 2011; Reygondeau and Beaugrand 2011) but only one also tried to identify the actual nature of these relationships (Carstensen et al. 2012). In this publication covering the Nordic Seas, a non-linear relationship of biomass and presence of *C. glacialis* with temperature was found, with constant values below and decreasing values above ~6 °C. *C. finmarchicus* biomass and presence on the other hand was mostly related to salinity and not to temperature (Carstensen et al. 2012). Daase et al. (2007) found significant correlations between temperature and abundance for both *C. glacialis* and *C. finmarchicus*, but their results might be affected by a correlation between temperature and salinity (Carstensen et al. 2012).

1.4.2 *Survival/mortality*

Most literature regarding the effect of temperature on survival/mortality is available for copepodite stages of *C. finmarchicus* (Clarke and Bonnet 1939; Hirche 1987; Tande 1988a; Campbell et al. 2001), whereas only one study has also investigated copepodite stages of *C. glacialis* (Hirche 1987), and one ntopliar stages of both species (Grenvald et al. 2013). In 24 hours lasting temperature experiments Hirche (1987) found somewhat lower acute tolerance for *C. glacialis* CV than for *C. finmarchicus* CV. We know of no further information on temperature-dependent mortality/survival for copepodite stages of *C. glacialis*. The results from studies investigating *C. finmarchicus* have been inconsistent. Tande (1988a) found that mortality of copepodites CI-CV was higher at 0.5 °C than at 3 °C and 6 °C, whereas Clarke and Bonnet (1939) found that mortality of stages CIII-CVI was lower at 3 °C than at 6 °C and 9 °C. Although Campbell et al. (2001) did not obtain accurate mortality rates, they found that

mortality of copepodites was lower at temperatures below 8 °C than at 12 °C. Naupliar mortality of *C. glacialis* and *C. finmarchicus* in response to pyrene and increasing temperatures has been investigated recently and those early developmental stages seemed very sensitive to increases in temperature (Grenvald et al. 2013). Daily mortality rates increased significantly with temperature in the control treatments for both species but more pronounced for *C. glacialis* (Grenvald et al. 2013).

1.4.3 *Growth and development*

Temperature strongly influences growth and development of ectotherms. Increasing temperatures lead to faster growth and decreasing development times. The most detailed assessment of the effect of temperature on growth and development has been done by Campbell et al. (2001) for *C. finmarchicus*. The authors estimated growth and development rates for almost the entire life cycle as a function of temperature and food quantity and quality. Unfortunately, they did not investigate the longevity or stage duration of adult stages.

No such detailed assessment exists for *C. glacialis* but studies on naupliar development indicate that *C. glacialis* develops faster at lower temperatures (below 2-3 °C) as compared to *C. finmarchicus* and slower at higher temperatures (Corkett et al. 1986; McLaren et al. 1988; Tande 1988a; Campbell et al. 2001; Daase et al. 2011; Grenvald et al. 2013). However, no such difference was found for lower temperatures in a recent investigation by Jung-Madsen and Nielsen (2015), assessing naupliar development of *C. glacialis* and *C. finmarchicus* from Disko Bay, western Greenland at temperatures between 0-10 °C. Instead, both species developed at similar rates below 5 °C, while above 5 °C *C. finmarchicus* developed faster than *C. glacialis* as has been shown previously. The faster naupliar development in Disko Bay could indicate local adaptation of *C. finmarchicus* to cold conditions (Jung-Madsen and Nielsen 2015).

1.4.4 *Feeding and faecal pellet production*

The number of studies on the effect of temperature on feeding and faecal pellet (FP) production rates of *C. glacialis* and *C. finmarchicus* is limited and the studies are partly difficult to compare due to different methodologies (Table 1). Unimodal responses in clearance rates are reported for *C. finmarchicus* females from Buzzards and Cape Cod Bay, Massachusetts, USA, by Anraku (1964) investigating a temperature range between 2 and 22.5 °C. Additionally, thermal optima varied with season, with highest clearance rates at 8 °C in May-July and at 15 °C in August, probably related to changes in *in situ* temperature (Anraku 1964). A unimodal response was also reported in a more recent study for *C. finmarchicus* CV collected in April in

Gullmarsfjorden, southern Sweden, by Møller et al. (2012), investigating a temperature range between 1 and 21 ± 0.5 °C. These authors found the highest clearance rates at 14 °C and estimated the thermal optimum to be 12.2 °C. In addition, they argue that the response in feeding to increasing temperatures is related to the relative development rate thereby affecting the distribution of *C. finmarchicus* (Møller et al. 2012).

To our knowledge no peer-reviewed literature exists investigating the thermal response of ingestion for *C. glacialis*, apart from **Paper I** and **II**, but Kjellerup et al. (2012) investigated FP production as an indicator for grazing of both, *C. glacialis* and *C. finmarchicus* from Disko Bay, Greenland, at a temperature range of 0-10 °C during three different bloom scenarios from March to May. Specific FP production under saturated food conditions was low in both species in the pre-bloom and post-bloom scenario and increased slightly until 7.5 °C, while rates decreased again at 10 °C. *C. finmarchicus* collected during the phytoplankton bloom in April significantly increased their specific FP production rates with increasing temperatures, whereas *C. glacialis* rates levelled off at temperatures above 7.5 °C (Kjellerup et al. 2012). Similar findings were obtained by Smolina et al. (2015) measuring adult female FP production under saturated food conditions during short-term (4 h) thermal stress response experiments in *C. glacialis* and *C. finmarchicus*, also from Disko Bay, Greenland, but at a temperature range of 0-15 °C. FP production increased from 0-10 °C for both species and levelled off for *C. finmarchicus* at 15 °C, while it strongly decreased again for *C. glacialis* at 15 °C (Smolina et al. 2015).

1.4.5 *Respiration*

Early work investigating the respiration of *C. finmarchicus* CV and adult females at temperatures ranging between 0-22.5 °C without food indicates generally increasing rates with increasing temperatures (Clarke and Bonnet 1939; Marshall and Orr 1958; Anraku 1964), but all individuals died within 24 hours at 22.5 °C (Anraku 1964). The same trend was found for *C. finmarchicus* females from the Fram Strait, Greenland Sea at experimental temperatures ranging between 0-18 °C, whereas respiration rates of *C. glacialis* CV increased at the lower temperatures and reached a plateau at ~10 °C (Hirche 1987). *C. glacialis* females from the Polar Front areas in the central Barents Sea on the other hand did not increase their respiration rates at *in situ* temperatures varying between -0.5 and 3.5 °C (Ikeda and Skjoldal 1989) nor at experimental temperatures between -1.7-5 °C, while the rates increased at 8 °C and 10 °C (Tande 1988b). In summary, respiration increased linearly at temperatures ranging from 0-18 °C for *C. finmarchicus* CV and adult females, whereas *C. glacialis* CV seemed to have

maximum respiration rates at 10 °C with no further increase with increasing experimental temperature, while for adult females no data exist for temperatures above 10 °C.

1.4.6 *Reproduction*

The effect of temperature on reproduction has received the most attention in the peer-reviewed literature available for *C. glacialis* and *C. finmarchicus* (Table 1). The reproductive traits of *C. glacialis* and *C. finmarchicus* that theoretically could be investigated in response to increasing temperature are mating behaviour and success, egg size, clutch size, daily egg production rates, total cumulative egg production (fecundity), and hatching success. Some of these traits are relatively difficult to investigate. Fecundity has to be obtained for the entire lifetime of the female, and investigating mating behaviour and success would require rather long incubation times. Daily egg production rates and hatching success however can be assessed relatively easy during incubation experiments and are therefore the most studied proxies of reproductive success (Table 1).

The earliest investigation of *C. finmarchicus* egg production rates at temperatures ranging between 5.3-13.5 °C with high food concentrations indicate an increase in rates with a Q_{10} coefficient of ~3 (Runge 1985). The Q_{10} temperature coefficient is a commonly used measure of the rate of change in biological or chemical rates because of a certain temperature increase (usually 10 °C). The most detailed assessment of the effect of temperature on reproduction has been done by Hirche et al. (1997) for *C. finmarchicus*. The authors estimated daily egg production rates, clutch size and spawning interval as a function of temperature, food quantity, and season. Daily egg production rates of females acclimated to 0 °C increased exponentially or linearly (same fit) at temperatures ranging between -1.5 and 8 °C and high food concentrations with a Q_{10} quotient of ~5, while the spawning interval decreased with increasing temperature (Hirche et al. 1997). No clear temperature effect on clutch size was detected but clutch size at 2 °C was significantly smaller than at 5 and 8 °C (Hirche et al. 1997). *C. glacialis* treated equally in experiments responded with a similar but less pronounced increase in daily egg production rates (Hirche and Kosobokova 2007). *C. finmarchicus* egg diameter and carbon content decreased significantly with increasing experimental temperature (4, 8, and 12 °C), while mean daily egg production rates and clutch size were lower at 8 °C as compared to 4 °C (Campbell et al. 2001). These authors explain the discrepancy to previous findings with the younger age of females at 8 °C that probably had not yet reached their full reproductive potential.

In addition to faecal pellet production rates, Kjellerup et al. (2012) also investigated egg production rates for both *C. glacialis* and *C. finmarchicus*. The specific egg production rates of *C. finmarchicus* generally increased with increasing temperature and under saturated food conditions, both when animals were collected during the phytoplankton pre-bloom and bloom, with the strongest increase during the bloom scenario. No effect was detected during the post-bloom scenario. *C. glacialis* had similar specific egg production rates during the pre-bloom and bloom, but during the pre-bloom the strongest increase occurred between 0-2.5 °C after which the rates levelled off, whereas during the bloom the strongest increase occurred between 5-7.5 °C. Generally, *C. glacialis* had higher egg production rates at lower temperatures (< 5 °C) as compared to *C. finmarchicus* (Kjellerup et al. 2012).

Two recent investigations could not find any effect of increasing temperatures (0-10 °C) on egg hatching success of *C. glacialis* and *C. finmarchicus* (Jung-Madsen and Nielsen 2015; Weydmann et al. 2015). However, hatching success was significantly reduced for *C. finmarchicus* eggs incubated at temperatures > 19 °C, while there was no effect on hatching success at temperatures between 6 °C and 19 °C (Preziosi and Runge 2014).

The distribution and success of a species depends on its ability to survive, grow, and reproduce under variable environmental conditions (Fig. 2). Increasing temperatures in the Arctic Ocean due to climate change will likely affect physiological processes of *C. finmarchicus* and *C. glacialis* differently, thereby altering the size-structure of the zooplankton community and the energy transfer to higher trophic level organism in the Arctic marine ecosystem. The aim of this thesis is to provide detailed knowledge about how changes in temperature affect different physiological activities of the copepod species *Calanus glacialis* (Arctic species) and *Calanus finmarchicus* (sub-Arctic species). Special focus is given to *C. glacialis,* as much less information is available for this species compared to *C. finmarchicus*. Ultimately, the thesis aims to investigate and discuss what the consequences of a warming Arctic Ocean for *C. glacialis* and *C. finmarchicus* populations may be by improving the thermal response parametrization in the SINMOD model system.

The main objectives of this thesis are to evaluate temperature effects 1) at the organismal level and 2) at the population level of *C. glacialis* and *C. finmarchicus*. The main objectives are separated into the following research questions:

1) How respond feeding rates of *C. glacialis*, as an indicator of metabolic gains, to increasing temperature? (**Papers I** and **II**)

2) How respond faecal pellet production rates of *C. glacialis*, as an indicator of metabolic losses, to increasing temperature? (**Paper I**)

3) Comparing feeding, faecal pellet production, and respiration rates, how does temperature affect the metabolic balance of *C. glacialis*? (**Papers I** and **II**)

4) How respond egg production rates of *C. glacialis* and *C. finmarchicus*, as an indicator of metabolic balance, to increasing temperature? (**Paper III**)

5) How does increasing temperature affect the biomass and productivity of *C. glacialis* and *C. finmarchicus* in the Barents Sea area? (**Paper IV**)

3.1 COLLECTION OF EXPERIMENTAL COPEPODS

Calanus glacialis and *C. finmarchicus* have been collected in summer 2009 and spring 2010 at different locations around the Svalbard Archipelago and in a fjord close to Tromsø, Northern Norway. For details, see Fig. 6 and Table 2.

3.2 *CALANUS* FEEDING AND METABOLIC BALANCE – PAPERS I AND II

3.2.1 *Material and methods*

In order to investigate the effect of increasing temperature on the ingestion rates of *C. glacialis* copepodite stage CV (**Papers I** and **II**) and adult females (**Paper II**), we performed short term incubation experiments (four hours) at five temperatures (0, 2.5, 5, 7.5 and 10 °C). In **Paper I**, we accounted for the recent feeding history (fed or starved for 3 days prior to the experiments) and *ad libitum*, high quality food conditions (diatom *Thalassiosira gravida*); whereas **Paper II** presents an *in situ* scenario regarding the feeding conditions (water from chlorophyll *a* maximum). The experimental set-up and calculation of ingestion rates are described in detail in **Papers I** and **II**. Copepods were acclimated for 2-4 hours, depending on the experimental temperature.

To be able to discuss the effect of increasing temperature on *C. glacialis* metabolic balance, we chose two different approaches for **Paper I** and **II**. In **Paper II**, respiration rates were measured for *C. glacialis* CV and adult females (AF) in incubation experiments at 0, 3, 6, and 10 °C following the method described in Alcaraz et al. (1998) and Almeda et al. (2011). For further details about the calculation of the Carbon-specific ingestion (C_I) and respiration rates (C_R) see **Paper II**. The metabolic balance was estimated as the difference between C_I as a proxy for energy gains and C_R as a proxy for metabolic losses.

In **Paper I**, we did not measure respiration rates but instead estimated Q_{10} values of ingestions for the whole experimental temperature interval (0-10 °C), as well as 0-5 °C and 5-10 °C and compared them with the Q_{10} values estimated from respiration measurements investigating similar temperature intervals (**Paper II**; Hirche 1987; Ikeda and Skjoldal 1989; Tande 1988b).
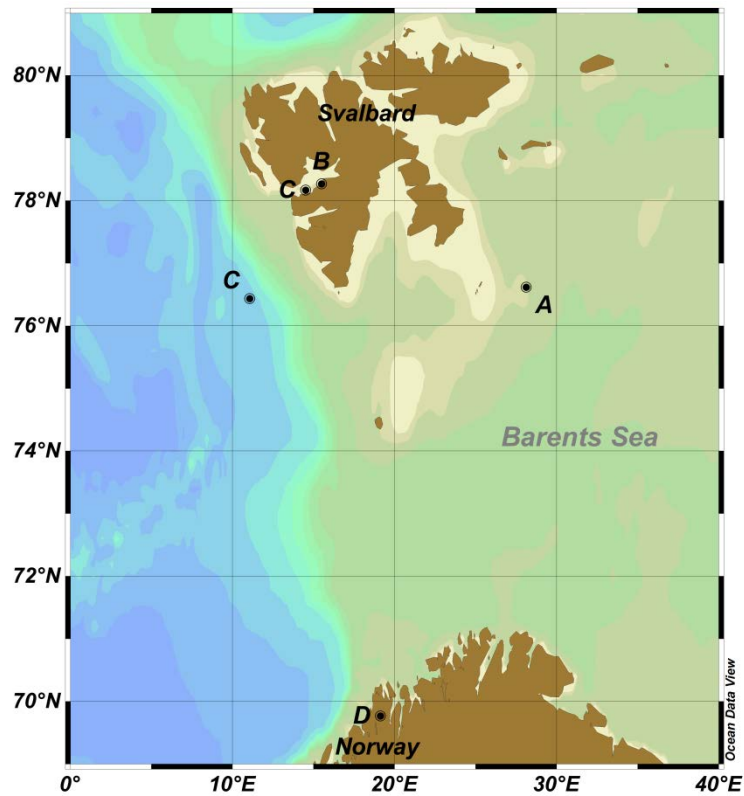
Fig. 6 Map over all sampling locations. A: Northern Barents Sea, *Calanus glacialis* sampled for **Paper II**. B: Adventfjorden, west coast of Spitsbergen, *C. glacialis* for **Paper I**. C: Isfjorden and west coast of Spitsbergen, *Calanus finmarchicus* and *C. glacialis* for **Paper III**. D: Grøtsund, northern Norway, *C. finmarchicus* for **Paper III**.

Table 2 Sampling overview for experiments of **Papers I**, **II**, and **III**. EPR = egg production rates

Paper	Sampling location	Sampling time	Species	Experiments
I	Adventfjorden (B)	July 2009	*C. glacialis*	Feeding
				Egestion
II	Barents Sea (A)	June 2009	*C. glacialis*	Feeding
				Respiration
III	West coast Spitsbergen / Fram Strait (C)	May 2010	*C. glacialis*	EPR
			C. finmarchicus	EPR
	Grøtsund (D)	March 2010	*C. finmarchicus*	EPR
		April 2010	*C. finmarchicus*	EPR
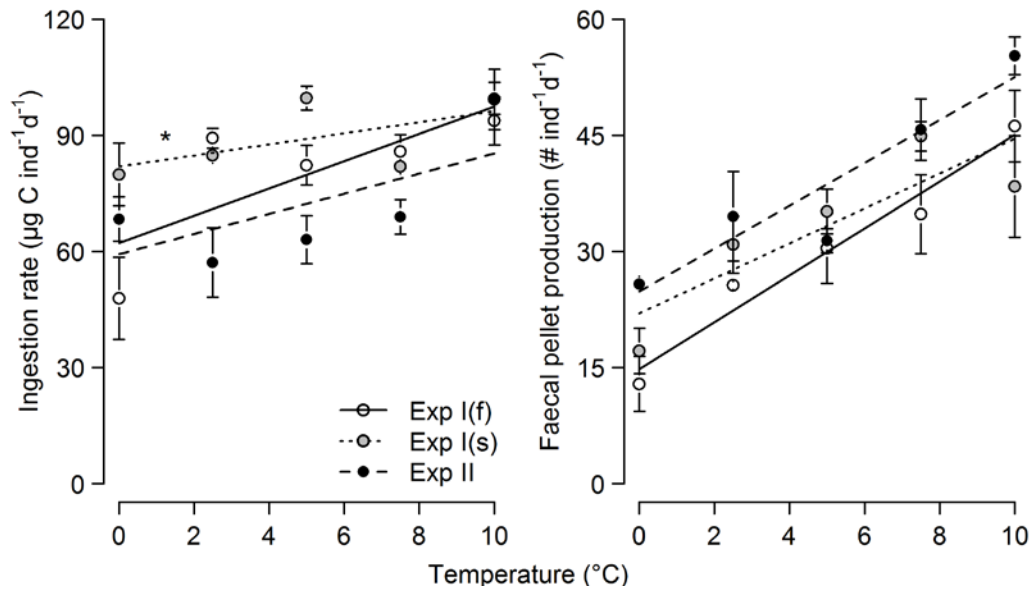
Fig. 7 Ingestion rates (µg C ind[-1] day^{-1}) and faecal pellet production rates (# ind[-1] day^{-1}) as a function of temperature for *Calanus glacialis* CV in three different experiments (experiment I pre-fed (f), experiment I pre-starved (s), and experiment II). The points represent mean values (± SE) and the lines represent linear regression lines, all of which were significantly increasing except ingestion rates in experiment I (s) indicated by *

3.2.2 *Main results*

In **Paper I,** ingestion and FP production rates generally showed a significant linear increase with increasing temperature and no optimum temperatures were detected (Fig. 7). No significant difference in ingestion rates between the two different feeding treatments (pre-fed vs. pre-starved) could be detected. However, the effect of temperature was significant in the pre-fed treatment but not in the pre-starved treatment (Fig. 7). Q_{10} values of ingestion were generally lower than Q_{10} values of FP production rates and published respiration rates (Table 3), indicating higher thermal sensitivity of ingestion compared to egestion and respiration.

Table 3 *Calanus glacialis* Q_{10} coefficients of ingestion (I) and faecal pellet production (E), for experiment I (Exp I) pre-fed (f) and pre-starved (s), experiment II (Exp II), and for published respiration rates : (1) Hirche 1987, Tab. 3; **Paper II**, Fig. 2; (2) Ikeda and Skjoldal 1989, Tab. 2; (3) Tande 1988, Fig. 2: ns = not significant

| Stage	T (°C)	Q_{10} I and E				Q_{10} R	Reference
		Exp. I (f)	**Exp. I (s)**	**Exp. II**			
CV	0 – 10.0	1.49	ns	1.45	(I)		**Paper I**
	0 – 5.0	1.65		1.50			
	5.0 – 10.0	1.35		1.40			
	0 – 10.0	3.05	2.03	2.12	(E)		**Paper I**
	0 – 5.0	4.09	2.29	2.43			
	5.0 – 10.0	2.27	1.79	1.85			
	0 – 5.0					4.60	(1)
	5.0 – 10.0					4.39	
	0 – 6.0[a]					4.37	**Paper II**
AF	- 0.5 – 3.5					3.43	(2)
	- 1.5 – 10.0					1.82	(3)

[a] **Paper II** presents a unimodal thermal response in respiration rates and the Q_{10} coefficient has been calculated for the temperature range below the optimum temperature.
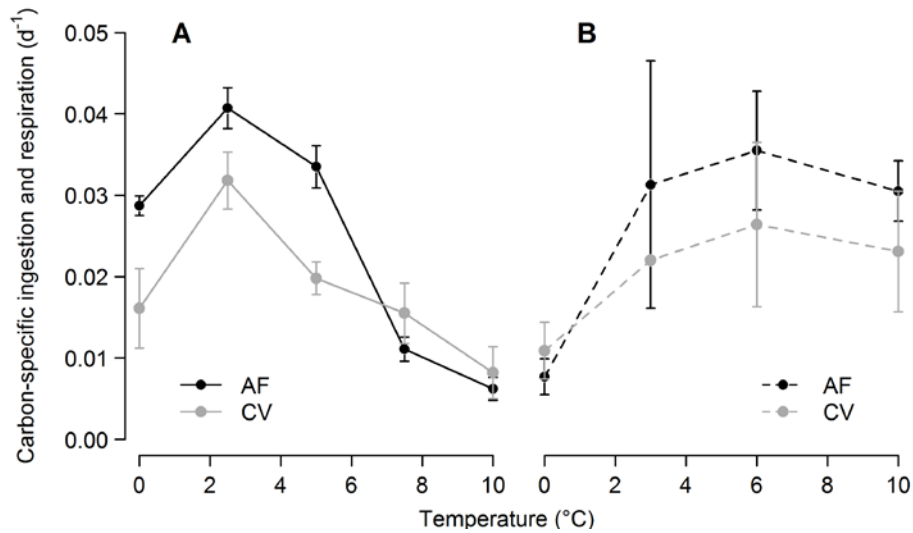
Fig. 8 *Calanus glacialis* copepodites V (CV) and adult females (AF) Carbon-specific ingestion (**A**) and respiration (**B**) in response to temperature. The points represent mean values (± SE)

In **Paper II** carbon-specific ingestion rates (C_I) increased until a thermal optimum at 2.5 °C for both developmental stages, whereas higher temperatures resulted in a decrease in C_I (Fig. 8A). Carbon-specific respiration (C_R) on the other hand increased until a thermal optimum at 6 °C for both developmental stages. Again, temperatures above the thermal optimum resulted in a decrease in C_R (Fig. 8B). The gross metabolic balance as a proxy of the total energy demand decreased continuously with temperature (Fig. 9). At approximately 5 °C, C_I could not cover the minimum C_R requirements for either CV or AF.
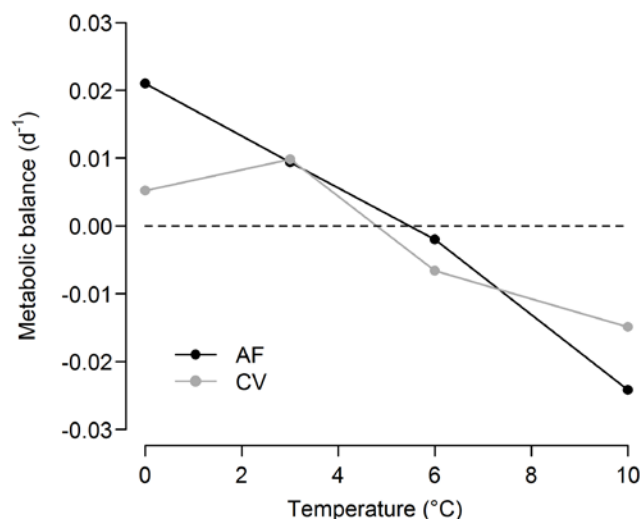
Fig. 9 Metabolic balance between ingestion (C_I) and respiration (C_R) in response to increasing temperature in *Calanus glacialis* copepodites V (CV) and adult females (AF)
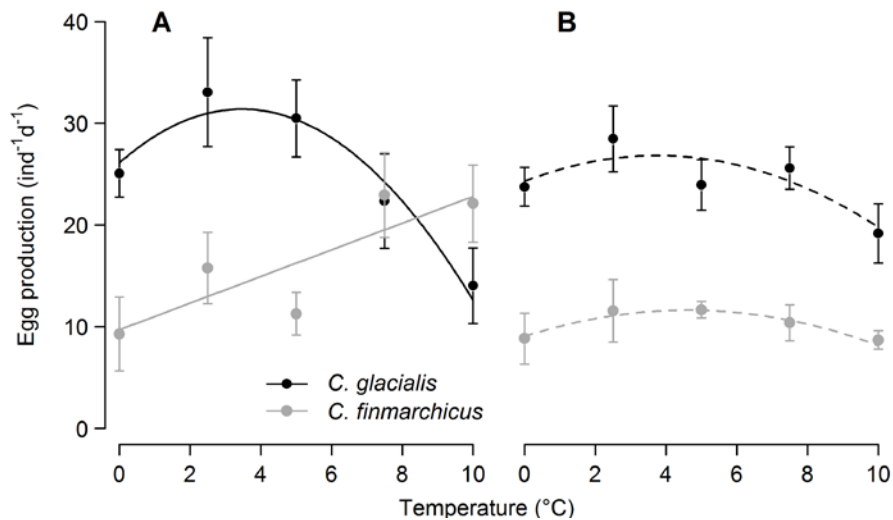
Fig. 10 *Calanus glacialis* and *C. finmarchicus* daily egg production rates (in May and April, respectively) in response to increasing temperature fed *ad libitum* the diatom *Thalassiosira gravida* (**A**) and starved during the experiment (**B**). Points = mean values (± SE); lines = fitted linear regression lines.

3.3   *CALANUS* EGG PRODUCTION – PAPER III

3.3.1   *Material and methods*

In order to investigate the effect of increasing temperature on *C. glacialis* and *C. finmarchicus* daily egg production rates (EPR), we performed long-term incubation experiments (5 days) with single females provided with either high food concentrations of the diatom *T. gravida* or no food. Daily EPR were assessed at five experimental temperatures (0, 2.5, 5, 7.5 and 10 °C) in March, April and May for *C. finmarchicus* and in May for *C. glacialis*. For details of the experimental setup, see **Paper III**.

3.3.2   *Main results*

EPR of fed *C. glacialis* females in May was highly depending on temperature and followed a unimodal pattern with a temperature optimum at 2.5-5 °C beyond which EPR strongly decreased again (Fig. 10A). EPR of fed *C. finmarchicus* females was highest in April and increased continuously within the investigated temperature range (Fig. 10A). Temperature dependence was much less pronounced in starved *C. glacialis* and *C. finmarchicus* females (Fig. 10B) and starved *C. finmarchicus* females laid significantly fewer eggs than fed females, whereas the presence of food had no significant effect on *C. glacialis*. Generally, *C. glacialis* had higher EPR compared to *C. finmarchicus* except at 7.5 °C and 10 °C under high food concentrations.

3.4   *CALANUS* POPULATION LEVEL RESPONSES – PAPER IV

3.4.1   *Material and methods*

We used a 1D water column ecosystem model setup (Wassmann et al. 2006) to investigate the effect of increasing water temperatures on different population parameters of *C. glacialis* and *C. finmarchicus* (**Paper IV**). We implemented the thermal unimodal responses identified in **Paper II** in feeding and respiration of *C. glacialis* and published thermal responses of *C. finmarchicus* feeding (Møller et al. 2012) and respiration (Hirche 1987) into existing structured population models of *C. glacialis* and *C. finmarchicus* (Slagstad and Tande 1990; 2007, respectively). The population models were introduced into the well-established coupled physical-biological SINMOD model system, replacing the simple box-models of the mesozoo-plankton compartment. Apart from investigating the effect of temperature on *C. glacialis* and *C. finmarchicus* populations, we compared the old, linear parametrization of the *Calanus* spp. feeding and respiration with our new, unimodal parametrization. Finally, we investigated the importance of plasticity related to thermal acclimation, as thermal responses of calanoid copepods may vary seasonally and spatially (Anraku 1964; Holste et al. 2009).

The structure of the *C. glacialis* and *C. finmarchicus* population models allowed us only to manipulate feeding and basal respiration, but not egg production, as *Calanus* spp. egg production is a direct function of feeding in the model. In the old parametrization, feeding of *C. finmarchicus* and *C. glacialis* was increasing exponentially with temperature, while respiration of *C. finmarchicus* was constant with temperature (Fig. 11). Respiration of *C. glacialis* nauplii was also constant with temperature, while respiration of copepodites increased exponentially. In the new parametrization, we used the unimodal feeding function by Møller et al. (2012) for *C. finmarchicus* and a unimodal feeding function fitted to the results from **Paper II** for *C. glacialis* (Fig. 11). For the temperature dependence of respiration, we used the exponential function provided by Hirche (1987) for *C. finmarchicus* and a unimodal respiration function fitted to the results from **Paper II** for *C. glacialis*.

The standard scenario simulations (no changes in temperature or thermal response) were run using atmospheric data from the European Centre for Medium-Range Weather Forecasts for the period 1989-2007 (19 years). However, only the last 13 years (1995-2007) were used for analysis, to exclude sources of variability in the simulated output variables due to the model spin-up time.
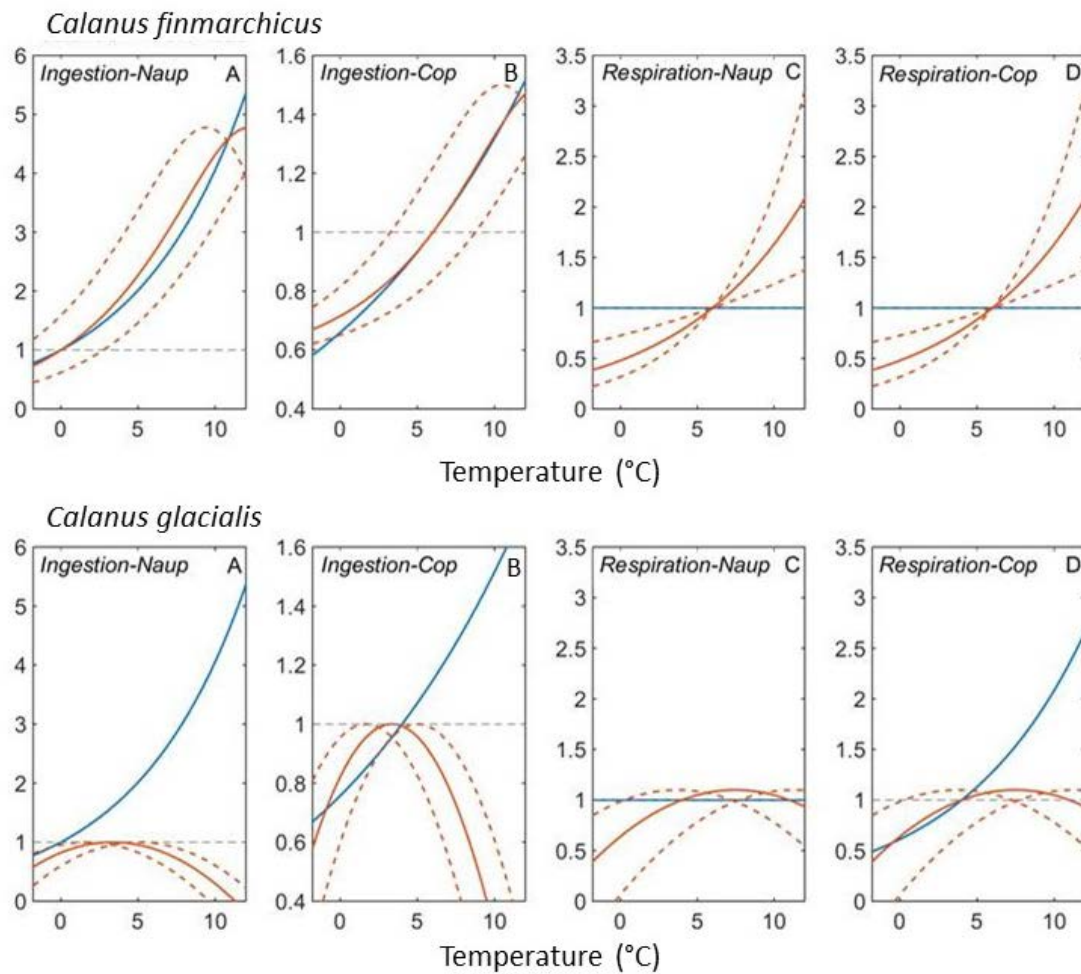
Fig. 11 Relation between normalized (to 1) modelled biological processes (ingestion and basal respiration) for nauplii and copepodite stages of *C. finmarchicus* (top) and *C. glacialis* (bottom) for the old parametrization (blue continuous line) and the new parametrization (red continuous line). Nauplii ingestion (A), copepodite ingestion (B), nauplii respiration (C), and copepodite respiration (D). The dashed lines represent the +/- 20% deviations from the standard parametrization of ingestion (A, B), and +/- 50% deviations from the standard parametrization of respiration (C, D) for the sensitivity analysis.

The simulations were performed at two different locations for each of the *Calanus* spp. (Fig. 12), characteristic for the currently known biogeographical extent of *C. finmarchicus* (St. 1 and 2) and *C. glacialis* (St. 3 and 4) in the Barents Sea region.

To assess the effect of increasing seawater temperature on different *Calanus* spp. population parameters, in addition to the standard temperature scenario, three modified temperature scenarios were implemented by artificially increasing the air temperature at the North Pole, resulting in four temperature scenarios: standard, +2 °C, +6 °C, and +8 °C.
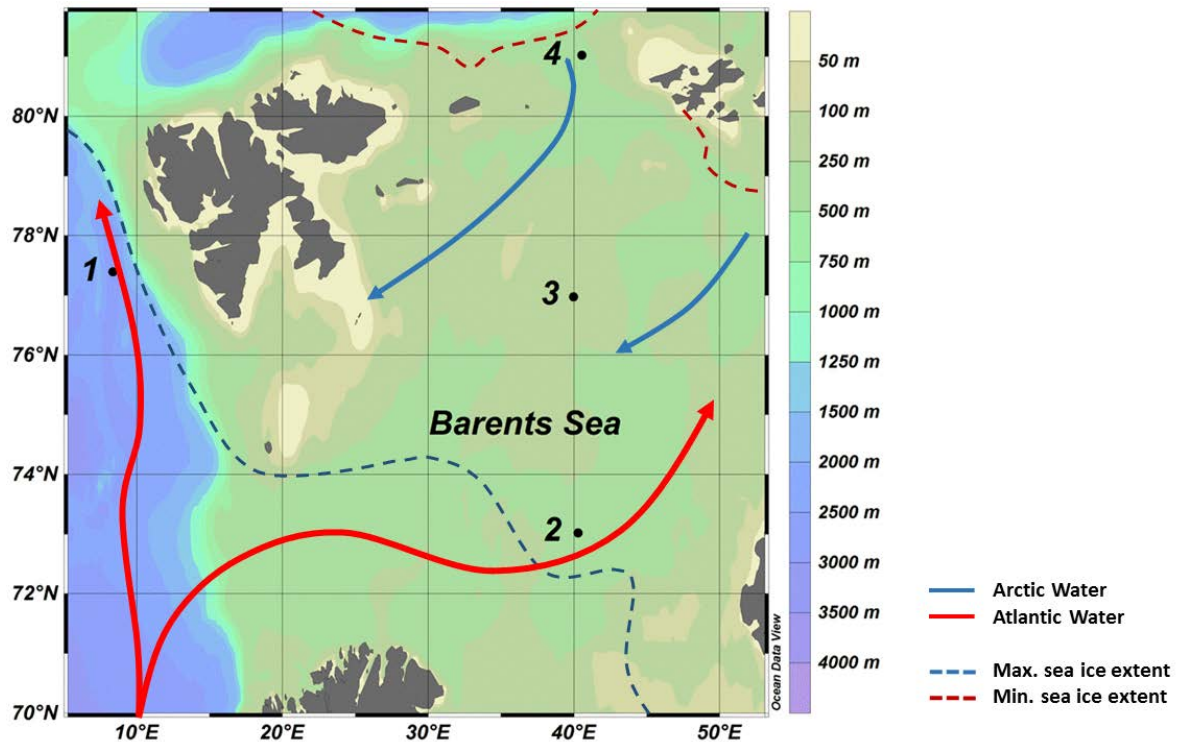
Fig. 12 Map of the grid cells (Stations 1-4) providing the input to the 1D water column ecosystem simulations. The direction and flow of Atlantic and Arctic ocean currents are indicated in red, solid lines (Atlantic) and blue, solid lines (Arctic). The dashed lines indicate the minimum (red) and maximum (blue) sea ice extent in April (1985-2014; Norwegian Polar Institute (2014)).

To investigate the sensitivity of *Calanus* spp. populations to changes in the new thermal feeding and respiration responses, simulating different thermal acclimations, we performed 1D simulations at the +8 °C temperature scenario, manipulating either the feeding or respiration parameter. We only manipulated the thermal optimum (unimodal) or slope (exponential) of the thermal responses (-50 %, -20 %, standard, +20 %, +50%), but did not change the general shape of the functions. The resulting *Calanus* spp. growth functions are shown in Fig. 13.

The investigated model outputs were average water temperature (upper 50 m), nauplii food concentration (mg C m^{-3}), copepodite food concentration (mg C m^{-3}), total population biomass (g C m^{-2}), total population net production (g C m^{-2} d^{-1}), adult female (AF) abundance (m^{-2}), and egg production rates (EPR, eggs fem^{-1} d^{-1}). All temperature and sensitivity simulation results were compared to the respective standard simulation. Only one factor was changed for each simulation and interacting responses were not addressed. In order to compare the different temperature and sensitivity scenarios, we calculated the annual population net production (g C m^{-2}), annual biomass (g C m^{-2}), annual AF abundance (m^{-2}), and annual EPR (eggs fem^{-1}). For more details regarding the simulations, see **Paper IV**.
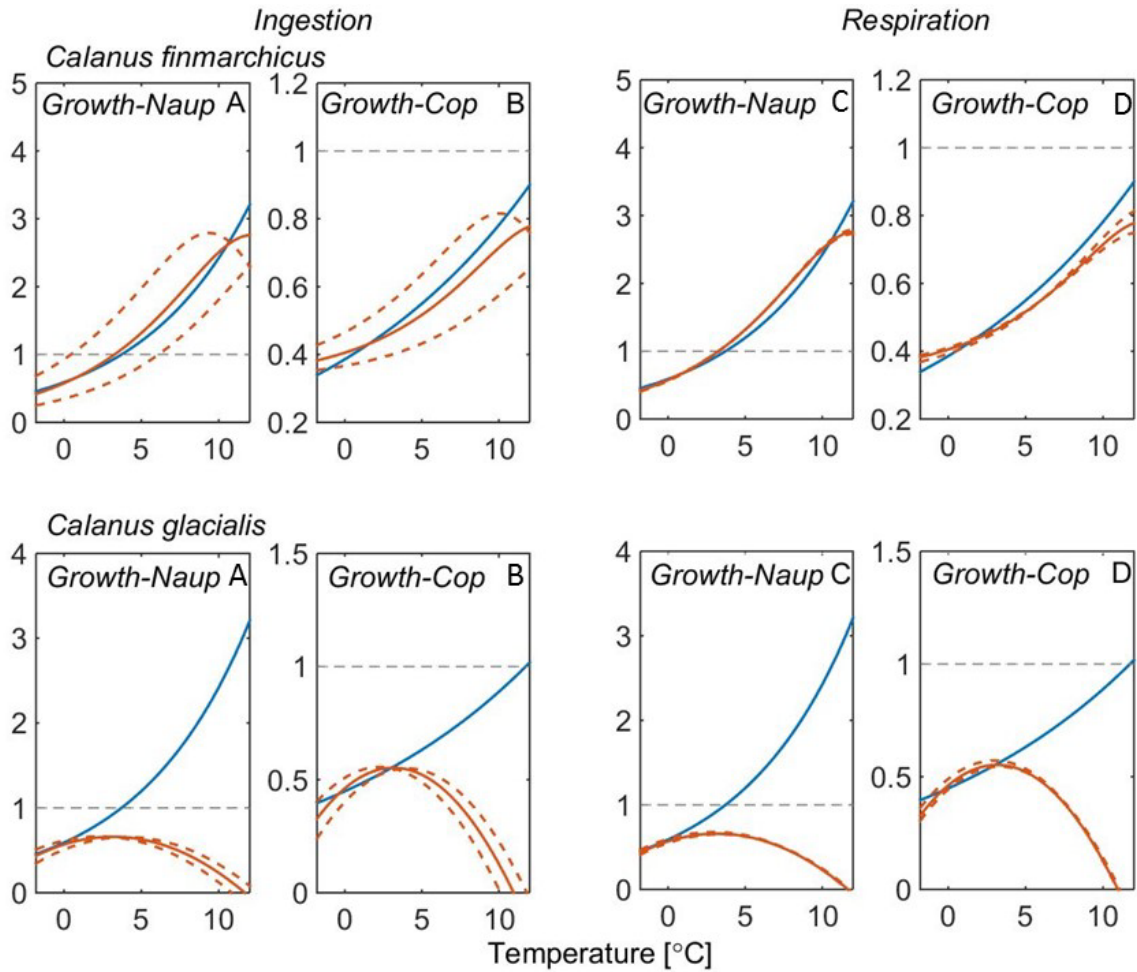
Fig. 13 The temperature dependence of net growth resulting from ingestion and basal respiration for nauplii and copepodite stages of *C. finmarchicus* (top) and *C. glacialis* (bottom) for the old parametrization (blue continuous line) and new parametrization (red continuous line). Dashed lines represent the +/- 20% deviations from the standard parametrization of ingestion (left panels), and +/- 50% deviations from the standard parametrization of respiration (right panels) for the sensitivity analysis.

3.5.2 *Main results*

Increasing the air temperature at the North Pole by +2 °C, +6 °C, and +8°C affected the average temperature in the uppermost 50 m of the water column of St. 1-4 differently (Figs. 14-17). Mean daily water temperatures increased on average gradually with increasing temperature scenario. Changes were most pronounced at St. 2 and 4 (4.3 ± 0.4 °C and 4.2 ± 1.3 °C average temperature difference between standard and +8 °C scenario, respectively), least at St. 3 (2.7 ± 1.3 °C) and intermediate at St. 1 (3.8 ± 0.6 °C).
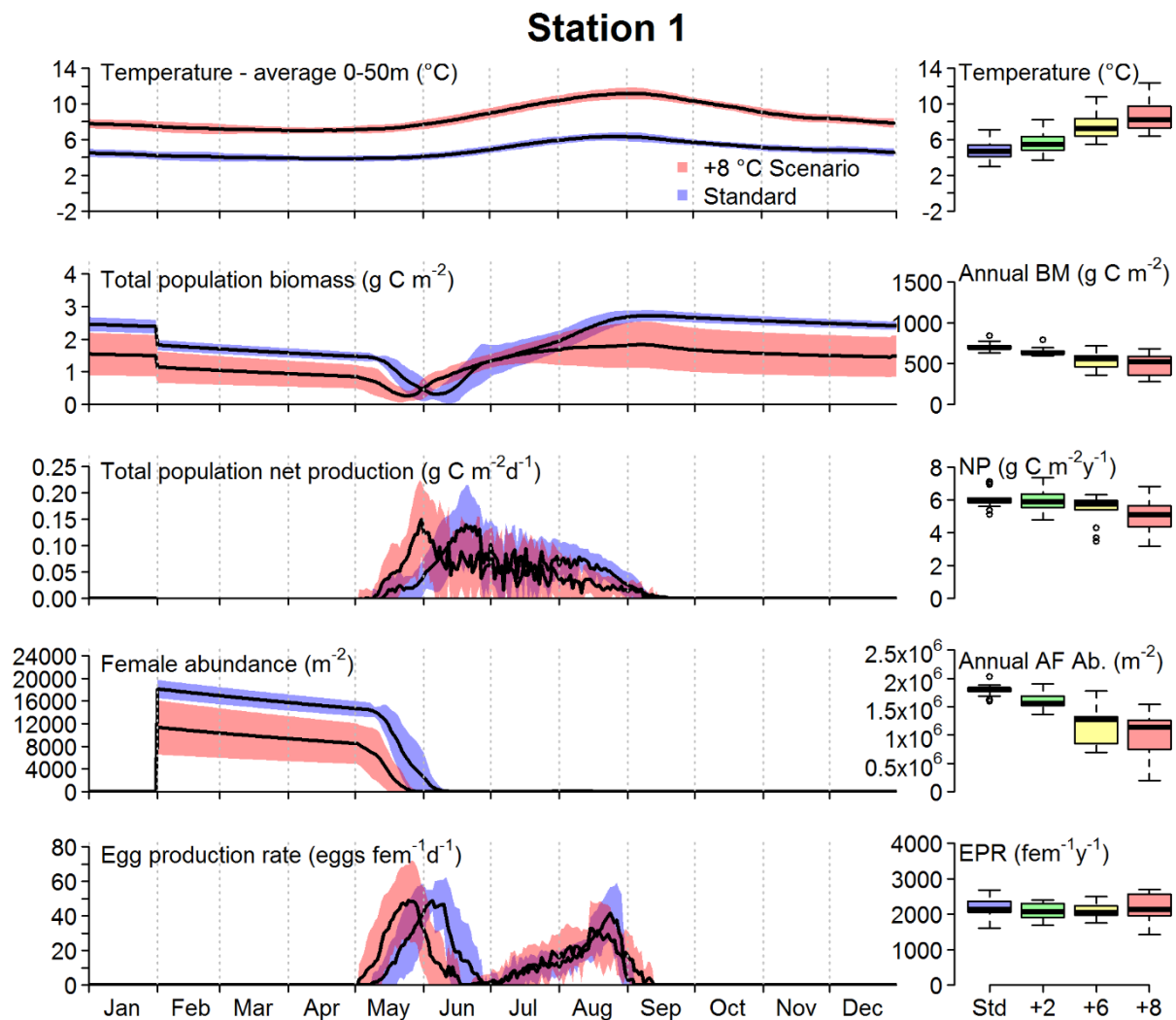
Fig. 14 Left panel: Simulated seasonal variability in average temperature (upper 50 m), total population biomass (g C m^{-2}), total population net production (g C m^{-2} d^{-1}), female abundance (m^{-2}), and egg production rates (eggs fem^{-1} d^{-1}) of *C. finmarchicus* at St. 1. Lines indicate daily means and confidence bands indicate one standard deviation. Blue bands represent the standard temperature scenario and red bands represent the +8 °C temperature scenario. **Right panel**: Box plots of simulated average temperature, Annual BM = annual biomass (g C m^{-2}), NP = net production (g C m^{-2} y^{-1}), Annual AF ab. = annual adult female abundance (m^{-2}), and EPR = egg production rates (eggs fem^{-1} y^{-1}) of *C. finmarchicus* at St. 1. Boxes display median ± 1 quartile (interquartile range IQR); whiskers denote highest and lowest data point still within the highest or lowest quartile + 1.5 IQR; open circles denote outliers and crosses the mean. All data from 1995 to 2007 combined.

Generally, increased temperature led to increased net production, biomass, AF abundance and EPR, as well as earlier maximum net productivity and EPR at St. 2-4 (Figs. 15-17). Especially for *C. glacialis*, the investigated parameters did not increase gradually with increasing temperature, but the strongest effects already occurred in the +2 °C and +6 °C temperature
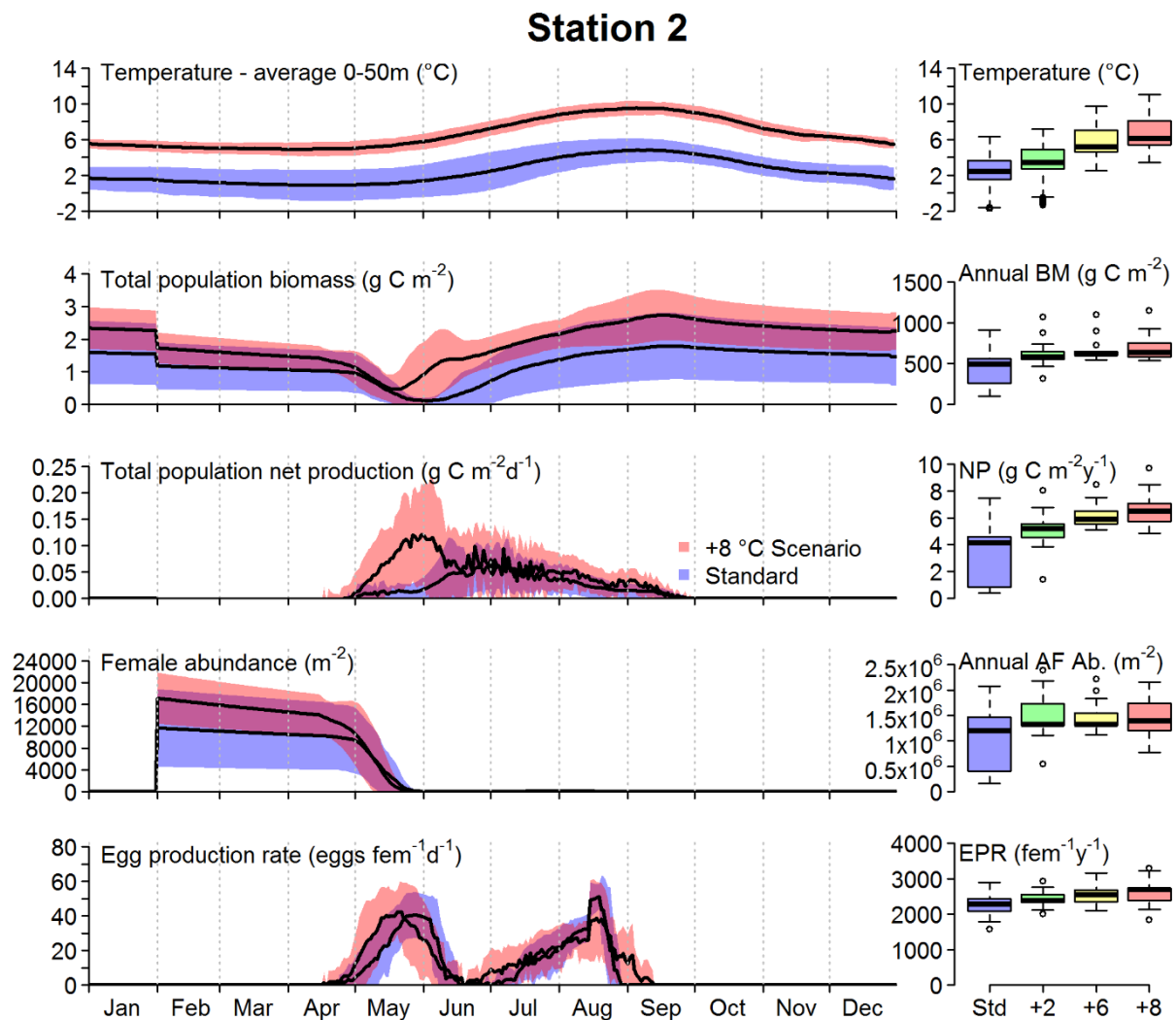
Fig. 15 Left panel: Simulated seasonal variability in average temperature (upper 50 m), total population biomass, total population net production, adult female abundance, and egg production rates of *C. finmarchicus* at St. 2. Lines indicate daily means and confidence bands indicate one standard deviation. **Right panel**: Box plots of simulated average temperature, Annual BM = annual biomass (g C m^{-2}), NP = net production (g C m^{-2} y^{-1}), Annual AF ab. = annual adult female abundance (m^{-2}), and EPR = egg production rates (eggs fem^{-1} y^{-1}) of *Calanus finmarchicus* at St. 2. All data from 1995 to 2007 combined. For details, see Fig. 11

scenarios, while the +6 °C and +8 °C scenarios were rather similar (Figs. 16 and 17), indicating considerable capability of *C. glacialis* to cope with increasing temperatures up to ~6 °C and even benefit from it.

In contrast, annual net production and biomass decreased with increasing temperature scenario for *C. finmarchicus* at St. 1 (Fig. 14, right panel), most likely due to decreasing primary productivity (not shown) induced by nutrient limitation.
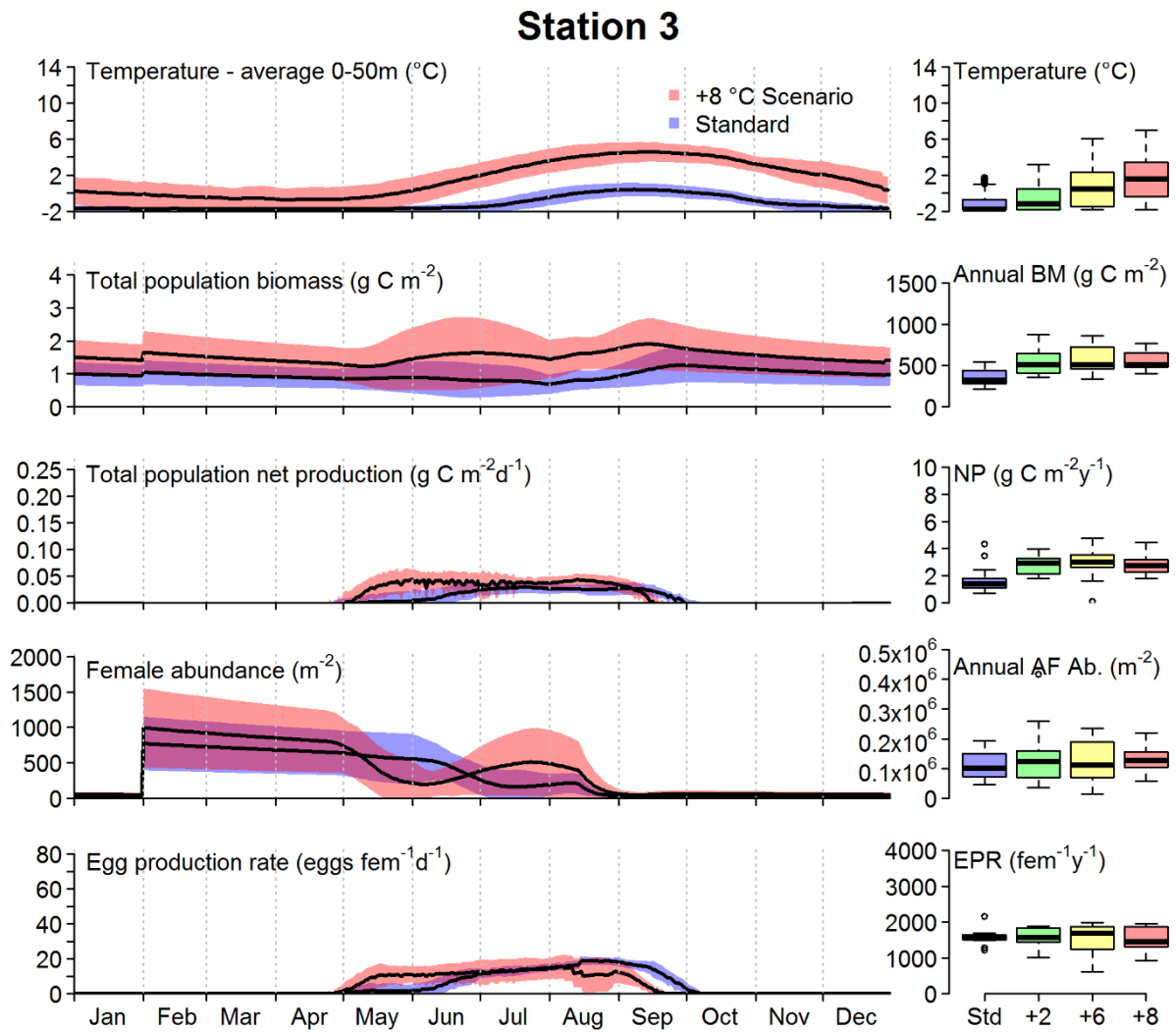
Fig. 16 Left panel: Simulated seasonal variability in average temperature (upper 50 m), total population biomass, total population net production, adult female abundance, and egg production rates of *C. glacialis* at St. 3. Lines indicate daily means and confidence bands indicate one standard deviation. **Right panel**: Box plots of simulated average temperature, Annual BM = maximum biomass (g C m^{-2}), NP = net production (g C m^{-2} y^{-1}), Annual AF ab. = annual adult female abundance (m^{-2}), and EPR = egg production rates (eggs fem^{-1} y^{-1}) of *Calanus glacialis* at Station 3. All data from 1995 to 2007 combined. For details, see Fig. 11

Changing the temperature optimum or curvature of the thermal response functions of feeding and respiration had no substantial effects on either *C. finmarchicus* or *C. glacialis* (results not shown).

As anticipated from the resulting growth functions (Fig. 13), the old and the new parametrizations did not differ substantially for *C. finmarchicus*, except for slightly higher annual net production in the standard and +2 °C scenarios (not shown). This is probably due to
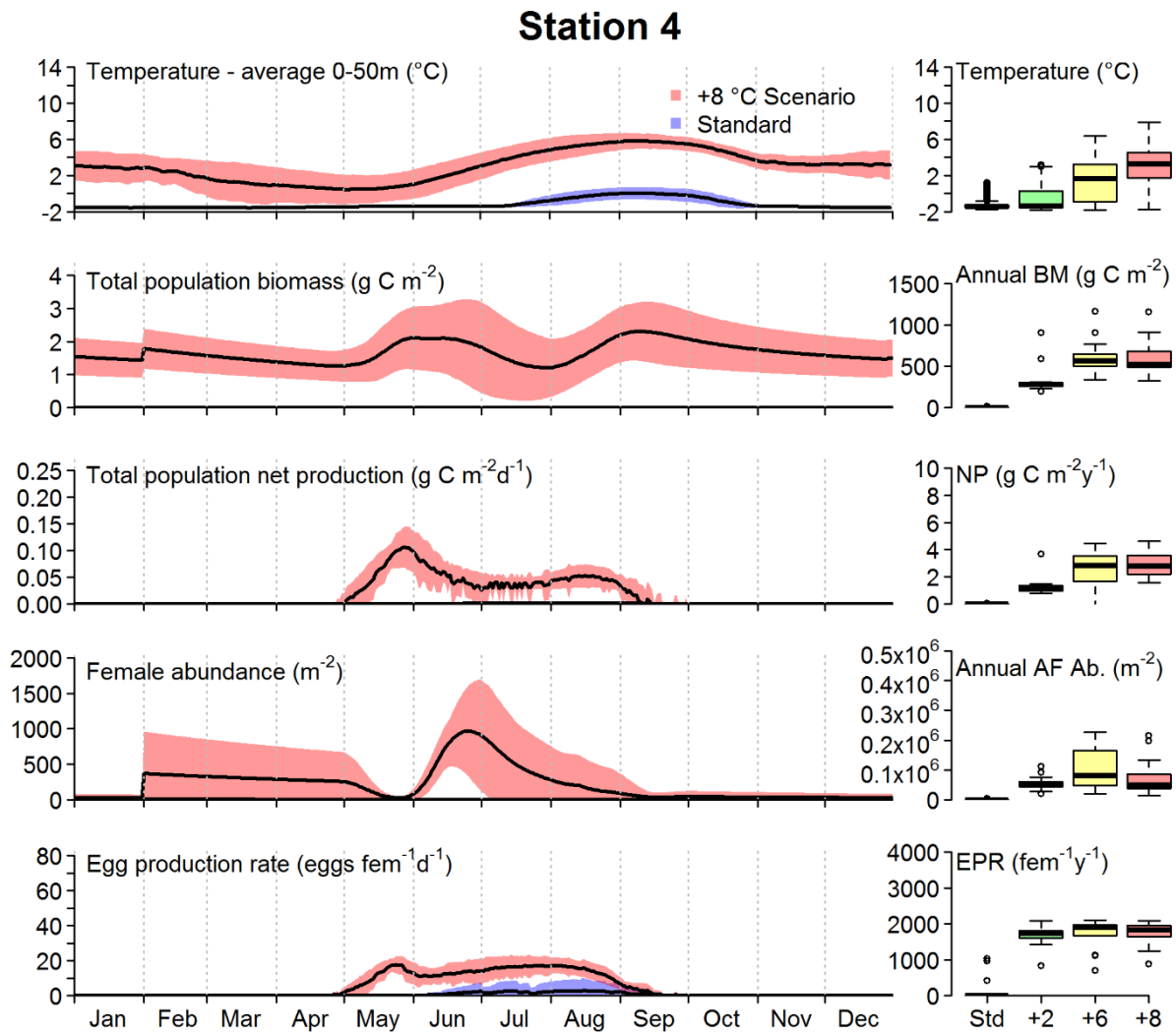
Fig. 17 Left panel: Simulated seasonal variability in average temperature (upper 50 m), total population biomass, total population net production, and egg production rates of *C. glacialis* at St. 4. Lines indicate daily means and confidence bands indicate one standard deviation. **Right panel**: Box plots of simulated average temperature, Annual BM = annual biomass (g C m^{-2}), NP = net production (g C m^{-2} y^{-1}), Annual AF ab. = annual adult female abundance (m^{-2}), and EPR = egg production rates (eggs fem^{-1} y^{-1}) of *Calanus glacialis* at St. 4. All data from 1995 to 2007 combined. For details, see Fig. 11

higher naupliar growth at 2-10 °C in the new parametrization as compared to the old parametrization (Fig. 13).

In contrast, the new parametrization substantially affected *C. glacialis* population parameters, with generally lower net production (Fig. 18), biomass (Fig. 18), AF abundance and EPR (not shown) in the new parametrization, especially in the +6 and +8 °C scenarios. This is most likely reflecting the new unimodal responses in feeding and respiration, compared to the exponential and constant responses in feeding and respiration in the old parametrization.
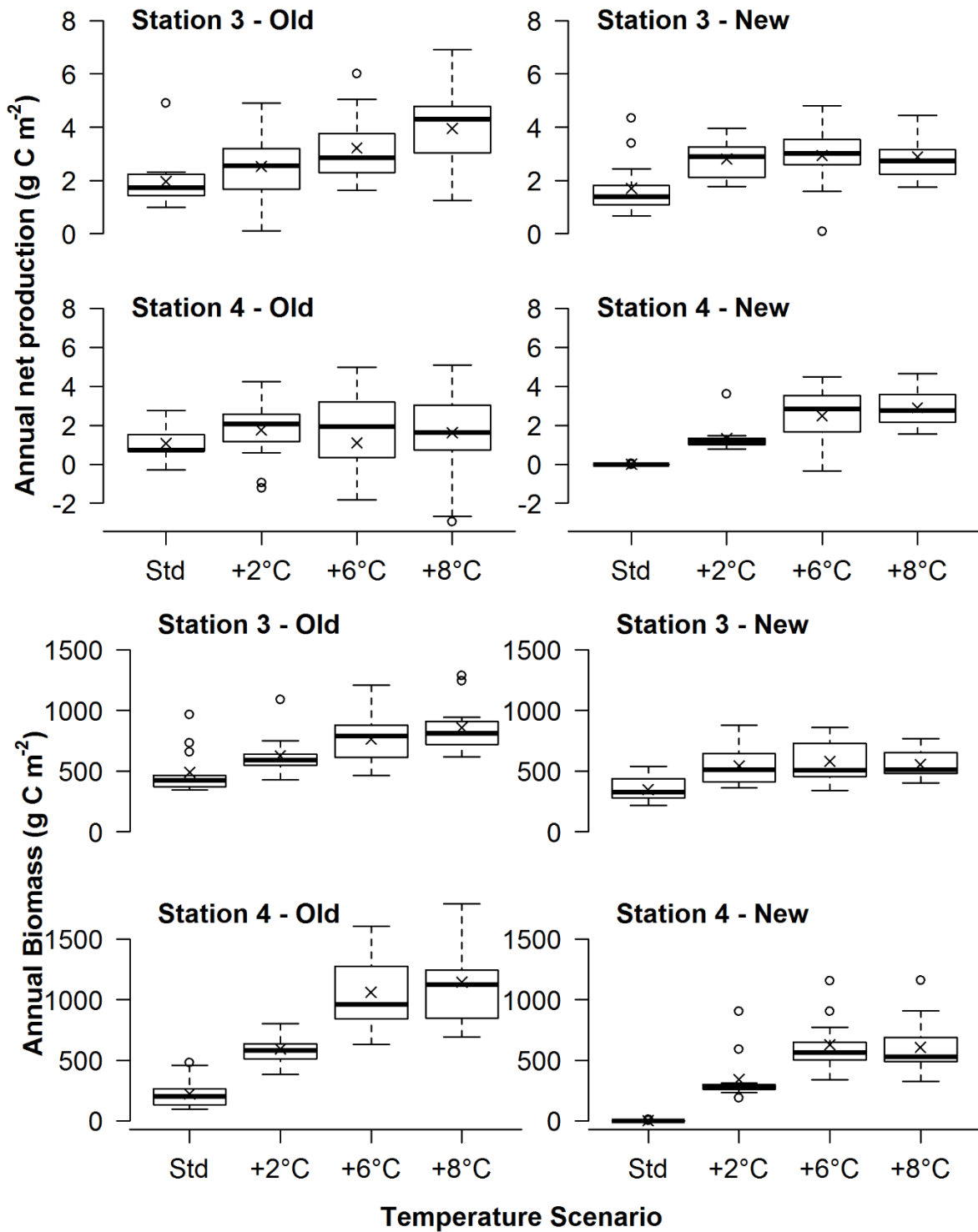
Fig. 18 Simulated annual net productivity (upper panels) and annual biomass (lower panels) of *Calanus glacialis* at St. 3 and 4 in the Barents Sea using the old parametrization (left panel) and the new parametrization (right panel). All data from 1995 to 2007 combined. Boxes display median ± 1 quartile (interquartile range IQR); whiskers denote highest and lowest data point that is still within the highest or lowest quartile + 1.5 IQR; open circles denote outliers and crosses the mean.

The performance of a species in relation to temperature depends on the thermal responses at the individual level (e.g. survival, growth, and reproduction) and the resulting responses at the population level (e.g. abundance and productivity). Depending on the ability of the individual organisms to survive, grow and reproduce under varying temperatures, the population will grow or decline. In addition, other environmental factors such as resource availability and/or predation pressure will affect population dynamics. In this thesis, I have focussed on the effect of increasing temperature feeding and reproduction of *Calanus glacialis* and *C. finmarchicus* experimentally at the individual level. I then implemented the obtained responses into an ecosystem model in order to achieve improved predictions about the population performance of *C. glacialis* and *C. finmarchicus* in a warming Arctic shelf sea.

4.1 TEMPERATURE EFFECTS ON THE ORGANISMAL LEVEL

4.1.1 *Effects of increasing temperature on feeding and faecal pellet production rates*

Feeding is fundamental for the performance of an organism, providing the energy for metabolism, growth, and reproduction. Additionally, an organism can only grow and reproduce if the metabolic gains (e.g. feeding) are higher than the metabolic losses (e.g. respiration).

Two different experimental investigations regarding the effect of increasing temperature on feeding of *C. glacialis* are part of this thesis, **Papers I** and **II**. In one experiment (**Paper I**) ingestion rates of *C. glacialis* increased linearly with increasing temperature (temperature range 0-10 °C), while in the other (**Paper II**) ingestion rates reached a temperature optimum at 2.5 °C, decreasing again at higher temperatures (temperature range 0-10 °C as well). The identified thermal responses in feeding, representing the metabolic gains, thus differ between the two experiments. Apart from the methodological differences (food source and concentration), differences in thermal acclimation might be implied as copepods have been sampled at different locations and different dates (Table 2). Seasonal differences in temperature optima were reported in clearance rates for *C. finmarchicus* females (Anraku 1964), as well as spatial differences (Anraku 1964; Møller et al. 2012).

Paper I also investigated the effect of temperature on egestion, i.e. faecal pellet (FP) production, as an indicator of metabolic losses. Similar to the ingestion rates, FP production of *C. glacialis* increased linearly with increasing temperature, but the increase was more pronounced than for the feeding response. Studies investigating the effect of temperature, food type and concentration on FP characteristics of calanoid copepods indicate that volume and density do not change considerably with changing temperatures, when using a single food type and high food concentrations (Feinberg and Dam 1998; Besiktepe and Dam 2002; Kjellerup et al. 2012), as was the case in our experiment (**Paper I**). Since temperature only affects the number of FP produced and egestion has a higher thermal sensitivity than ingestion, our study suggests that assimilation efficiency decreases with increasing temperature in *C. glacialis*. A decrease in assimilation efficiency with increasing temperature would in turn lead to less energy being available for metabolism, growth and reproduction. Using FP production as an indicator for feeding can be problematic when investigating temperature effects as it might overestimate feeding at warmer temperatures.

Copepod FP contribute significantly but with varying intensity to the particulate organic carbon (POC) transport to depth (Turner 2015). However, often FP seem to be retained in the upper 200 m of the water column (Turner 2015), most likely by the combined effects of microbial degradation, and ingestion or mechanical breakup by copepods and protozooplankton (Svensen et al. 2012). The degradation of the FP retains organic material and nutrients in the upper water column, thereby possibly prolonging the pelagic productive season (Svensen et al. 2012). A relative increase in FP production due to higher temperatures might strengthen the carbon transport to depth and/or retention processes.

4.1.2 *Effects of increasing temperature on metabolic balance*

The metabolic balance or energetic balance of an organism depends on the energetic outcome of processes governing metabolic gains (e.g. ingestion, assimilation efficiency) and metabolic losses (e.g. respiration, excretion, and egestion). We investigated the metabolic balance of *C. glacialis* and *C. finmarchicus* in response to increasing temperature in multiple ways.

In **Paper I** we compared the Q_{10} values of experimentally determined ingestion and egestion rates to published respiration rates (**Paper II**; Hirche 1987; Ikeda and Skjoldal 1989; Table 3). The Q_{10} values obtained imply that egestion and respiration (metabolic losses) had a higher thermal sensitivity than ingestion (metabolic gains) (**Paper I**). If ingestion does not increase as pronounced with increasing temperature as egestion and respiration, relatively less energy can be allocated to growth and reproduction at higher temperatures.
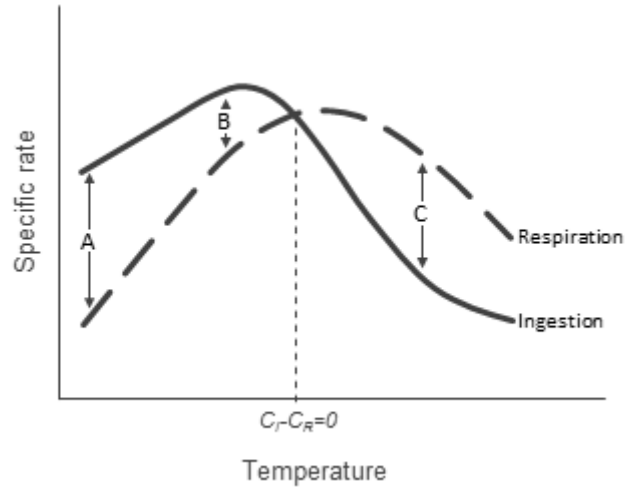
Fig. 19 Conceptual figure of the results from **Paper I** and **II** illustrating three possible temperature scenarios: **A**) At relatively low temperatures the metabolic balance is positive as the carbon specific ingestion rate is higher than the respiration rate, allowing for growth and reproduction. **B**) With increasing temperature relatively less energy is available for growth and reproduction as the respiration rate increases more pronounced than the ingestion rate (**Paper I**). **C**) The metabolic balance becomes negative at relatively high temperatures potentially resulting in negative effects on survival (**Paper II**).

Since we obtained unimodal thermal responses in ingestion and respiration in **Paper II**, calculating Q_{10} values was not meaningful. We therefore calculated the carbon specific respiration and ingestion rates in order to be able to compare respiration and ingestion directly. The carbon specific respiration rate had a higher thermal optimum than the carbon specific ingestion rate, resulting in a thermal limit for growth and reproduction at approximately 6 °C, above which ingestion could not fulfil the minimum respiration requirements of *C. glacialis* copepodite stage V (CV) and adult females (AF). The temperature response of the metabolic balance thus differs between the two studies (**Paper I** and **II**). A conceptual summary of the results obtained in **Paper I** and **II** is illustrated in Fig. 19, visualizing three different possible scenarios and highlighting the importance of the thermal window investigated. At relatively low temperatures, the metabolic balance is positive, as the carbon specific ingestion rate is higher than the respiration rate, allowing for growth and reproduction (Fig. 19, scenario A). With increasing temperature, relatively less energy is available for growth and reproduction as the respiration rate increases more drastically with temperature than the ingestion rate (Fig. 19, scenario B), as shown in **Paper I**. The metabolic balance becomes negative at relatively high temperatures leading to a metabolic mismatch and survival could consequently be negatively affected (Fig. 19, scenario C), as presented in **Paper II**.

Adult females of *C. finmarchicus* and *C. glacialis* have reached the final stage of development and invest their energy into egg production instead of growth (Runge and Roff 2000). Egg production rates (EPR) can therefore be an indicator of the relative amount of energy available for growth and should reflect the resulting thermal response of metabolic gains and losses to some degree, depending on the importance of internal lipid stores for egg production. Both, *C. glacialis* and *C. finmarchicus* can utilize up to 50% of their lipid stores for gonad maturation (Hirche and Kattner 1993; Jónasdóttir 1999). While *C. finmarchicus* generally depends on food to fuel spawning (Falk-Petersen et al. 2009), *C. glacialis* shows a more flexible reproductive strategy, capable of income breeding (fuelled by food) and capital breeding (fuelled by internal lipid stores), depending on the timing and type of primary production (Daase et al. 2013; Hatlebakk 2014). Yet, even when food is available, both species seem to fuel spawning with internal lipids (mainly wax esters), and *C. glacialis* females from Greenland were shown to refuel their lipid stores, while actively spawning during algae blooms (Swalethorp et al. 2011). Consequently, EPR of *C. glacialis* probably only represent a fraction of the energy available for growth, as copepods might invest in energy storage instead.

Experimentally obtained EPR of *C. glacialis* in May 2010 from the west coast of Svalbard (**Paper III**) indicate a thermal optimum between 2.5-5 °C (Fig. 10). At temperatures above 5 °C, relatively less energy is available for reproduction, indicating higher thermal sensitivity in processes governing metabolic losses, as opposed to processes governing metabolic gains. The findings for *C. glacialis* in **Paper III** are therefore in agreement with the findings in **Papers I** and **II**. *C. finmarchicus* EPR increased linearly with temperature, indicating no imbalance between metabolic losses and energy uptake within the temperature range investigated, in accordance with previous findings (Hirche et al. 1997; Kjellerup et al. 2012).

In summary: The physiological responses of *C. glacialis* to increasing temperature compared to *C. finmarchicus* include:

1.   slower development (Corkett et al. 1986; Daase et al. 2011; Grenvald et al. 2013),
2.   lower feeding rates (**Papers I** and **II**; Kjellerup et al. 2012; Smolina et al. 2015),
3.   lower egg production rates (**Paper III**; Kjellerup et al. 2012), and
4.   higher naupliar mortality (Grenvald et al. 2013).

This suggests that a warmer Arctic Ocean will likely favour *C. finmarchicus* over *C. glacialis*.

## 4.2   TEMPERATURE EFFECTS ON THE POPULATION LEVEL

While the response of single organisms to increasing temperature is relatively straightforward to investigate experimentally, investigating the response of a population experimentally is generally not as simple. In order to evaluate effects of increasing seawater temperatures on the *Calanus* spp. population level, one has to consider complex interactions between for example physical processes, physiological processes, developmental stages, and trophic interactions. Numerical modelling provides a powerful tool to perform such complex investigations.

We have used the coupled physical-ecological SINMOD model to assess the effect of increasing seawater temperatures due to climate warming on *C. glacialis* and *C. finmarchicus* population parameters in the Barents Sea region (**Paper IV**). To improve the thermal response parametrization of the model, we implemented the experimental physiological responses of *C. glacialis* (respiration and feeding, **Paper II**) into the model. We chose the ingestion rates obtained in **Paper II** over those from **Paper I** because of the additional respiration parameters measured and because *C. glacialis* included in this study were sampled in the Barents Sea in similar cold conditions as computed in the simulations. The feeding responses reported in **Paper II** are therefore more likely to represent realistic responses for the simulations.

The simulations (**Paper IV**) show a clear increase of *C. glacialis* production and biomass with increasing temperature at the two stations in the Barents Sea. This is in stark contrast to previous simulation experiments using SINMOD (Ellingsen et al. 2008; Slagstad et al. 2011; Slagstad et al. 2015), which predicted a strong decrease of *C. glacialis* in the northern Barents Sea at similar temperature scenarios. The strong temperature limitation of *C. glacialis* in those previous simulations does however not rely on observed physiological constraints but is based on an additional temperature dependent mortality parameter, simulating higher predatory mortality at temperatures above 4 °C due to high abundances of e.g. capelin and cod in the warmer water masses of the Barents Sea (pers. comm. D. Slagstad).

The constant and relatively low mortality of *Calanus* spp. assumed in our simulations is one of the main practical constraints of the model regarding the simulated parameters, especially biomass, as the model generally only considers bottom-up effects on *Calanus* spp. However, top-down processes (predation by e.g. fish) can have a significant effect on mesozooplankton biomass (Dalpadado et al. 2012). Fish in turn experience the same impacts of climate variability as zooplankton, such as direct physiological impacts (metabolism, reproduction), and indirect impacts through their biotic (prey, predator, and species interacting dynamics) and abiotic environment (habitat type and structure).
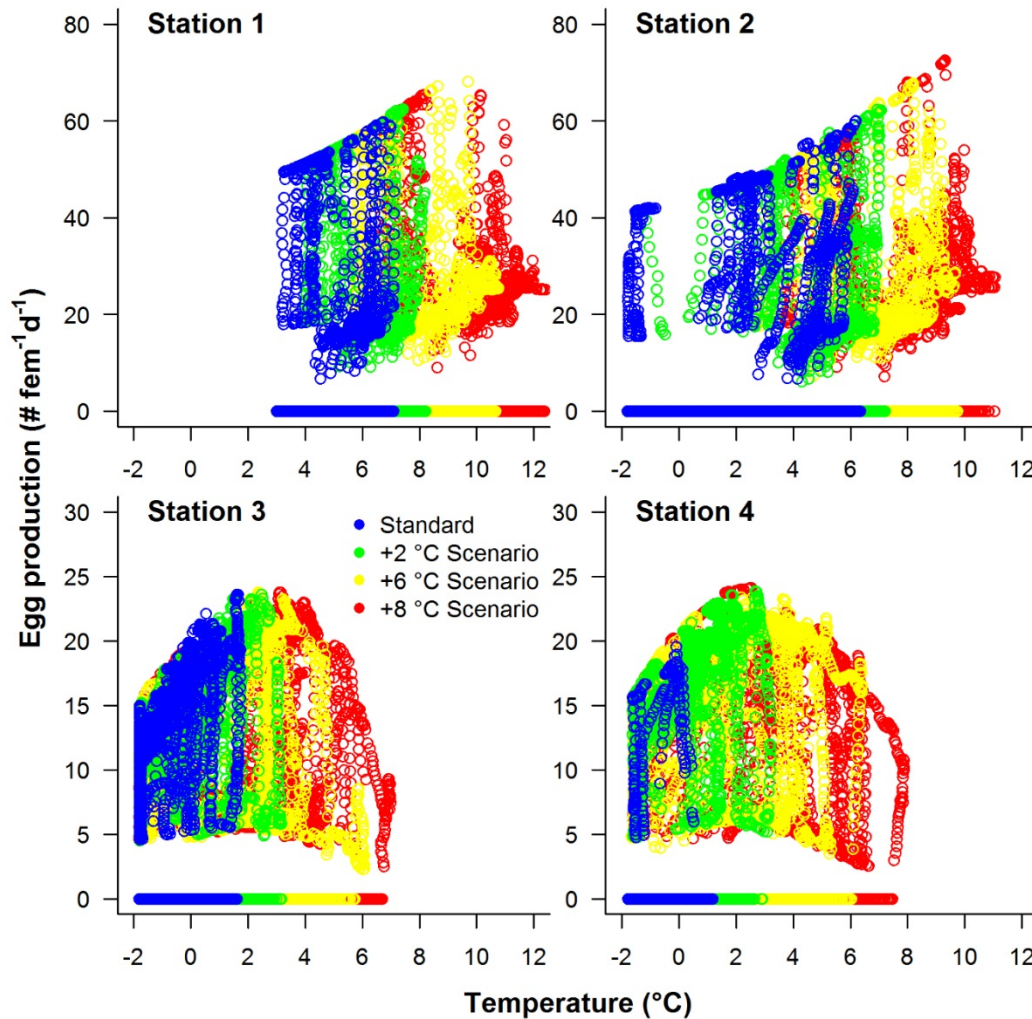
Fig. 20 Simulated daily egg production rates of *Calanus finmarchicus* (Stations 1 and 2) and *C. glacialis* (Stations 3 and 4) as a function of seawater temperature in the Barents Sea region. Blue = standard temperature scenario; green = +2 °C scenario; yellow = +6 °C Scenario; red = +8 °C scenario.

The aim of the sensitivity analysis was to investigate the effect of different thermal acclimations in feeding and respiration on *Calanus* spp. populations. Changing the basal respiration response generally affected net growth less than changing the ingestion response (Fig. 13), as ingestion, together with the active respiration, contribute more to the net growth than basal respiration in the model. Overall, the outcome of the analysis was limited as we only assessed the effect of different thermal optima kept constant throughout the year and with unchanged performance breadth or maximum performance, in contrast to observed thermal responses in calanoid copepods during different seasons and at different locations (e.g. Anraku 1964; Holste et al. 2009).

As discussed in the previous section, in adult females, which no longer grow, the amount of energy, which is otherwise allocated to growth, is invested at least to some degree into egg production. In the model, net growth is a function of ingestion, assimilation efficiency (constant), active respiration and basal respiration and EPR is a function of net growth divided by egg mass. In the simulations, EPR should therefore reflect the potential growth resulting from ingestion and respiration (Fig. 13) and ideally, the EPR observed in our experiments (**Paper III**; Fig. 10).

Simulated EPR reflect the simulated net growth and shape of the thermal response observed for EPR in **Paper III** reasonably well (Fig. 20). However, simulated maximum EPR (40-70 eggs fem^{-1} day^{-1}; Fig. 20) were much higher for *C. finmarchicus* than observed maximum EPR in our experiment (10-20 eggs fem^{-1} day^{-1}; Fig. 10). While mean EPR of up to 70 eggs fem^{-1} day^{-1} have been observed at 8-10 °C (Hirche et al. 1997; Kjellerup et al. 2012), in agreement with our simulations, observed mean EPR by others did not exceed 30 eggs fem^{-1} day^{-1} at 0 °C (Hirche et al. 1997; Kjellerup et al. 2012), staying well below maximum simulated EPR. This indicates that the model overestimates EPR of *C. finmarchicus* at lower temperatures. Simulated maximum EPR of *C. glacialis* (15-25 eggs fem^{-1} day^{-1}; Fig. 20) are on the other hand generally lower than our observed maximum EPR (25-40 eggs fem^{-1} day^{-1}; Fig. 10). While mean EPR of 10-15 eggs fem^{-1} day^{-1} have been observed at 0 °C (Hirche and Kosobokova 2007; Kjellerup et al. 2012), in agreement with our simulations, observed mean EPR exceeded 40 eggs fem^{-1} day^{-1} at 8-10 °C. This indicates that the model underestimates EPR of *C. glacialis* at higher temperatures. Consequently, *C. finmarchicus* biomass and net production could be overestimated at lower temperatures (e.g. standard simulation at St. 2), while *C. glacialis* biomass and net production could be underestimated at higher temperatures (e.g. +8 °C scenario at St. 4).

In summary: The simulated response of *C. glacialis* and *C. finmarchicus* populations to increasing water temperatures indicates that:

1. *C. finmarchicus* biomass and net production will likely increase in the southern Barents Sea, while

2. *C. glacialis* biomass and net production will likely increase in the northern Barents Sea up to water temperatures of 5-6 °C during summer.

3. Further warming will very likely reduce *C. glacialis* biomass and net production due to a metabolic mismatch negatively affecting growth.

4. While physiological responses to increasing temperature play an important role for *Calanus* spp., changes in food availability due to nutrient limitation will have more pronounced effects on population biomass and productivity, suppressing the potentially positive effects of initially increasing temperatures.

In this thesis, I investigated and discussed environmental parameters affecting *Calanus* spp. feeding, egestion, respiration and reproduction. All these parameters affect population growth. However, the spatial and temporal variation in copepod abundance is not only determined by population growth, but also by population decline due to mortality. Copepods experience both predatory and non-predatory mortality. Predatory mortality can be influenced by factors such as predator abundance, predator type (e.g. visual or tactile), and copepod adult abundance (cannibalism), stage and size, which in turn are affected by environmental conditions and seasonal variation (Peterson and Kimmerer 1994; Ohman and Wood 1995; De Robertis et al. 2000; Ohman and Hirche 2001; Eiane and Ohman 2004; Ohman et al. 2008). Non-predatory mortality of copepods on the other hand, is influenced by factors such as diet (e.g. starvation, harmful algae blooms), injuries, viral and parasite infections, pollution, and other environmental stressors (Daase et al. 2014 and references therein).

In addition, senescence contributes to non-predatory mortality, although probably to a much smaller degree. Generally, adult copepod longevity decreases with increasing temperature (Gophen 1976; Uye 1981; Hirst and Kiørboe 2002; Isla et al. 2008). Temperature may therefore act indirectly on predatory mortality and, both indirectly and directly, on non-predatory mortality. The peer-reviewed findings regarding the direct effects of temperature on non-predatory mortality are summarized in Table 1. However, estimating daily mortality rates is not sufficient when investigating the effect of temperature on mortality, as development time generally decreases with increasing temperature in marine planktonic copepods (Hirst and Kiørboe 2002; Huntley and Lopez 1992). Mortality rates should thus be estimated relative to stage duration (Hirst et al. 2007), as increasing daily mortality rates with increasing temperature may simply translate into constant stage-specific survival. Unfortunately, no peer-reviewed publications exist regarding the stage duration/longevity of *C. finmarchicus* and *C. glacialis* adult females.

Grenvald et al. (2013) found that daily mortality rates of naupliar stages of *C. glacialis* and *C. finmarchicus* increased significantly with increasing temperature (0, 5, and 10 °C) and the increase was more pronounced for *C. glacialis*. Interestingly, the latter effect remained after I corrected for the provided estimated development times, indicating that stage-specific survival

of naupliar stages of *C. glacialis* was in fact negatively affected by increasing temperature, whereas stage-specific survival of naupliar stages of *C. finmarchicus* was lowest at 0 °C. *Calanus* spp. simulated biomass and net production have been shown to be sensitive to higher constant or episodic increases in mortality in the SINMOD model (Skardhamar et al. 2011). Changes in mortality affected *C. glacialis* and *C. finmarchicus* differently, depending on the life cycle and habitat (Skardhamar et al. 2011). Our limited knowledge of predatory and non-predatory mortality rates for the key zooplankton species *C. glacialis* and *C. finmarchicus* and how these rates vary spatially, temporarily and between developmental stages, therefore limits our ability to predict population level impacts of changing mortality rates. Additional important knowledge gaps that need to be addressed in the future are the stage duration of adult females of *C. glacialis* and *C. finmarchicus* (i.e. adult female longevity), preferably at different temperatures, as well as long-term incubations (e.g. several weeks) investigating the thermal response of mortality rates of *C. glacialis* and *C. finmarchicus* copepodite stages.

In the context of climate change in the Arctic Ocean, *C. finmarchicus* distribution is clearly not limited by its physiological responses to increasing seawater temperatures. In contrast, *C. glacialis* distribution in the Barents Sea, to our current knowledge, seems to be restricted to water temperatures below 5 – 6 °C (Carstensen et al. 2012; **Papers I**, **II**, **III** and **IV**). This is in agreement with observations made in the Norwegian Lurefjord (Niehoff and Hirche 2005), White Sea (Kosobokova 1999), and St. Lawrence Estuary (Parent et al. 2015), where adult females stopped spawning and left the surface waters when temperatures reached approximately 5 °C. In contrast, no such thermal limitation has been observed in *C. glacialis* populations from Disko Bay, western Greenland (Niehoff et al. 2002; Kjellerup et al. 2012). The different thermal responses observed in feeding (**Paper I** and **II)** and in EPR (**Paper III**; Kjellerup et al. 2012) from different locations indicate local adaptation in *C. glacialis*. Phenotypic plasticity is therefore an important factor for the (local) adaptability of a species, i.e. its capability to persist and adapt to environmental changes. Yet, in the current thesis relatively little attention was paid to plasticity and the adaptive potential, especially of *C. glacialis*. Our approach to investigate the influence of plasticity in thermal responses on population biomass and production (**Paper IV**) was limited by the lack of available data and assuming unchanged thermal responses throughout the whole simulation period. In order to assess the importance of phenotypic plasticity and (local) adaptability of *C. glacialis*, long-term studies, covering different seasons, need to be conducted at different locations. To be able to differentiate between these two mechanisms, so-called common garden experiments would be

required. These experiments need to run over several generations and are therefore challenging with relatively long-lived organisms such as *C. glacialis*, requiring well established cultures and facilities. Numerical models are powerful and promising tools but the simulations should be based on physiological data.

When comparing physiological responses of *C. glacialis* and *C. finmarchicus*, reliable species identification is essential. Traditionally, both species have been separated based on the frequency distribution of prosome length within each copepodite stage (e.g. Kwasniewski et al. 2003; Arnkværn et al. 2005; Forest et al. 2011). Recently developed molecular identification methods revealed however a substantial overlap in prosome length between the two species (Lindeque et al. 2006; Parent et al. 2011), in addition to temporal and spatial variation in overlapping prosome length (Gabrielsen et al. 2012). In the Svalbard area, *C. glacialis* is frequently misidentified as *C. finmarchicus* when identification is based on prosome length, due to the presence of small sized *C. glacialis* (Gabrielsen et al. 2012). A reliable morphological feature to discriminate live *C. glacialis* from *C. finmarchicus* females from Greenland, which was also used in this thesis, is the red pigmentation of the antennae (Nielsen et al. 2014). However, to date it is not clear whether this morphological feature also applies to other areas, such as the Barents Sea. Therefore, I cannot exclude that *C. glacialis* has been misidentified as *C. finmarchicus* and vice versa, but misidentification is probably low, as we picked only large individuals with marked pigmentation for experiments with *C. glacialis*.

Generally, size is a plastic trait, mainly controlled by growth and development rates. In many ectothermic species individuals maintained at lower temperatures attain larger body sizes at maturity than when reared at warmer temperatures, the so-called temperature-size rule (TSR; Atkinson 1994). This phenotypic plasticity is one of the possible explanations for the Bergman clines, that is the increasing trend in body size along geographical gradients with decreasing temperatures, which has been recently also shown for *C. glacialis* and *C. finmarchicus* (Leinaas et al. 2016). Temperature was identified as the main driver for the pronounced differences in size between *C. glacialis* individuals from Lurefjorden (southern Norway) and different Arctic fjords in Svalbard (Leinaas et al. 2016). Increasing seawater temperatures are thus likely to lead to smaller body size in *C. glacialis*, similar in size to *C. finmarchicus* and presumably also lipid content. The traditional view that the large, energy-rich, Arctic *C. glacialis* could be replaced by the small, less energy-rich, Atlantic *C. finmarchicus* in a warming Arctic Ocean (Falk-Petersen et al. 2007) is partly challenged by this.

This thesis provides detailed insights into how temperature differently affects important physiological processes such as feeding, egestion, respiration and egg production in two important *Calanus* species. It further indicates that the balance between these processes is of high importance when it comes to the thermal sensitivity of especially *C. glacialis*. The results presented in this thesis indicate that *C. glacialis* will likely be able to benefit from moderate increases (up to 5-6 °C) in seawater temperature in the Barents Sea and probably also in other Arctic shelf seas. The results also signify that food availability plays a crucial role in a future warming Arctic Ocean, probably outweighing initially advantageous temperature effects. While *C. glacialis* shows the potential to benefit from moderate temperature increases, it is also likely to become smaller and correspondingly less lipid rich. Changes in the size structure of key zooplankton species such as *C. glacialis* will likely have pronounced negative consequences for Arctic marine species depending on lipid rich copepods, such as little auks, polar cod, and bowhead whales.

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