



Impact of salinity and temperature on the vital rates of co-occurring *Calanus glacialis* and *C. finmarchicus* from West Greenland

Maria Makri^{1,*}, Per Juel Hansen², Torkel Gissel Nielsen¹

¹National Institute of Aquatic Resources-DTU Aqua, Kemitorvet, Building 202, 2800 Kgs. Lyngby, Denmark

²Marine Biological Section, University of Copenhagen, Strandpromenaden 5, 3000 Helsingør, Denmark

ABSTRACT: Climate change creates multiple stressors for organisms in Arctic ecosystems, such as key zooplankton species of the genus *Calanus*. Here, we quantified the mortality and fecal pellet production rate of *Calanus finmarchicus* and *C. glacialis* from Disko Bay, West Greenland, with respect to temperature and salinity. The 2 species were exposed to temperatures of 0, 5 and 10°C and a salinity range from 5 to 60. *C. glacialis* had a significantly lower mean lethal concentration (LC₅₀) of 9 with a standard error of 1.98 at the lowest temperature, at salinities below *in situ* salinities, compared to *C. finmarchicus* (14 ± 0.35). At high temperatures, *C. glacialis* LC₅₀ was significantly lower than that at 0°C. At high salinities, the 2 species did not have significantly different LC₅₀ values. The fecal pellet production rates were quantified at saturated food concentration (> 400 µg C l⁻¹). No impact of salinity was observed between salinities of 25 and 40. Increases in fecal pellet production rates were observed at the limits of this range, indicating a physiological stress response. Within the 25–40 salinity range, fecal pellet production rates increased exponentially with temperature for *C. finmarchicus* (average Q₁₀ = 1.9 ± 0.18) in the temperature range of 0–10°C, while for *C. glacialis*, they peaked at 5°C (average Q₁₀ between 0 and 5°C was 2.19 ± 0.15). Our results demonstrate a high physiological plasticity of both *Calanus* species with respect to salinity. *C. glacialis* will be more tolerant in a future surface freshening scenario, although this advantage seems to be impaired at temperatures above 5°C.

KEY WORDS: Climate change · Zooplankton · Trophic cascades · Acute mortality · Ingestion rates · Q₁₀

1. INTRODUCTION

The combination of climate change and other anthropogenic stressors poses many challenges to Arctic and subarctic marine ecosystems. Decreasing albedo effects cause air temperatures in the Arctic to increase at rates much faster than in other regions (AMAP 2021). Sea surface temperatures, under a business-as-usual scenario, respond diversely according to the area, with hotspots of warming, such as the area east of Newfoundland, and cooling, such as the subpolar gyre to the south of Greenland, con-

sequently affecting species distribution, habitat, and phenology (McGinty et al. 2021). A general increase in the freshwater input to the Arctic Ocean is projected due to an increase in precipitation and glacial meltwater, which increases riverine input, and a decrease in sea-ice export (Pierce et al. 2012). Sea surface salinities in coastal areas are decreasing in the Arctic (Sejr et al. 2017), which, in combination with increased sea surface temperatures, will intensify stratification (Capotondi et al. 2012).

Marine zooplankton, especially copepods, are significant constituents of the marine pelagic food web,

*Corresponding author: mamak@dtu.dk

as they convert and transfer energy from lower trophic level organisms to higher trophic levels. In addition, they are sensitive indicators of environmental changes in marine ecosystems, as their physiological activities depend on environmental variables, including temperature and salinity. Hence, slight changes in these variables significantly affect their physiology, with cascading effects on their community structure, diversity and population size. The distribution of different zooplankton species inside subarctic fjord systems has been correlated to the influence of hydrography and glacial meltwater (Arendt et al. 2010, Calbet et al. 2011, Tang et al. 2011a,b, Middelbo et al. 2018). In subarctic waters, where Atlantic and Arctic water masses meet, the Atlantic species *Calanus finmarchicus* (Gunnerus, 1770) and the Arctic shelf species *C. glacialis* Jaschnov 1955 are the dominant copepod species (Tande et al. 1985, Hirche 1991, Hirche & Mumm 1992). Salinity and temperature vary seasonally in coastal Arctic and subarctic waters; during the winter months, the upper 100 m of the water column are usually well mixed and characterized by uniform salinity of about 33 and a temperature around -1°C (Weslawski et al. 1988, Hansen et al. 2012). With the retreat of sea ice and the increase in irradiance in spring, a phytoplankton bloom develops in the nutrient-rich surface layer. Studies on various fjord systems where *Calanus* spp. are present have shown a similar pattern with a gradual establishment of a halocline due to the influence of glacial meltwater, accompanied by simultaneous warming of the surface waters. Surface salinities close to glaciers vary from 30 to 10 during summer (Bendtsen et al. 2014, Stuart-Lee et al. 2021). Surface temperatures at the end of August can reach as high as 13°C (Riisgaard et al. 2014), while a cold subsurface layer is formed due to the glacial meltwater influence.

Calanus spp. are adapted to the seasonality of food availability in the Arctic, by storing wax esters, and other lipids, to fuel hibernation in deep waters during the winter (Ashjian et al. 2003, Kvile et al. 2019) and reproduction the following spring (Falk-Petersen et al. 1987, 2009, Lee et al. 2006). There is a positive linear correlation between the total amount of lipids in a *Calanus* individual and its prosome length (Renaud et al. 2018). *C. glacialis* reaches a larger prosome length (Choquet et al. 2018), leading to larger amounts of stored lipids in females. Through the accumulation of lipids, this genus constitutes a key link between the primary production and higher trophic levels in Arctic and subarctic ecosystems (Falk-Petersen et al. 2009), although inferences on trophic relationships

made from lipid composition analyses should be made with caution (Clarke et al. 1987). Their responses to climate change are therefore important in understanding and predicting future changes in Arctic food webs.

Disko Bay is located on the West Coast of Greenland (69°N , 53°W), and it marks the southernmost border of the Arctic Sea ice, showing seasonal sea ice coverage with high interannual variability (Hansen et al. 2006). The effects of climate change on temperature and salinity in the Bay are evident in the area over the past decades. During the period 1991–2004, mean annual temperatures in the Bay increased by 0.4°C (Hansen et al. 2006). Since 1997, an intensified melting of the Ilulissat glacier has been reported (Thomas 2004), leading to an acceleration of the meltwater input in the Bay area (Holland et al. 2008). Following an oceanographic regime shift, marked by a significant increase in the inflow of warmer Atlantic water and a decrease in sea ice coverage in Disko Bay (Hansen et al. 2012), the contribution of *C. finmarchicus* females to the total *Calanus* female biomass in the Bay has increased from 39 to 64% (Møller & Nielsen 2019). The effects of such a shift on pelagic productivity and carbon sequestration are complex, since the species vary not only in lipid content, but also in life cycle and generation time (Renaud et al. 2018).

Studies on *C. glacialis* have identified ice algae as an important nutritional source for females during spring (Runge & Ingram 1988, 1991). Microalgal blooms form an algal layer at the underside of pack ice, where salinities can be as high as 50, as well as inside the brine pockets and channels, where salinity ranges from values of 60 to 90 (Grant & Horner 1976). In the early spring, *C. glacialis* individuals feed actively inside or near the ice–water interfacial layer (Runge & Ingram 1988, 1991). During the ice melting, with a subsequent freshening of the surface waters, ice algae are released in the water column and *C. glacialis* ceases to migrate to the surface (Runge & Ingram 1991). The extent to which *C. glacialis* is exposed and can tolerate the cold, relatively fresh water of the ice melt or the high salinities at the sea ice–water interface during its feeding on the ice algal bloom remains uncertain.

The impact of climate change and other anthropogenic influences on the composition of the *Calanus* community has been a subject of many previous studies (Hjorth & Nielsen 2011, Grenvald et al. 2013, Rodríguez-Torres et al. 2020), but the physiological responses of the 2 species to salinity changes remain to be investigated. Elevated temperatures as high as 10°C have been associated with increased egg pro-

duction rates in *C. finmarchicus*, while temperatures over 5°C at the beginning of summer have coincided with arrested reproduction and initiation of female dormancy in *C. glacialis* in the White Sea (Kosobokova 1999) and in Lurefjord, western Norway (Niehoff & Hirche 2005). With increasing surface temperatures and intensified stratification, temperatures in the surface water layer exceeding 6°C are expected to be more persistent (AMAP 2021). By feeding on ice algae, *C. glacialis* is also subject to high salinities encountered close to brine pockets and channels.

This study aims to identify the combined effects of a wide range of salinities and temperatures, corresponding to a future, highly stratified, warmer, and fresher Arctic, as well as the conditions close to the ice–water interface, on the acute mortality and fecal pellet production rates of the 2 *Calanus* species adapted to the conditions prevailing in Disko Bay, West Greenland. The thermal sensitivity of both species' physiology, in combination with unfavorable salinity conditions, were evaluated by calculating the Q_{10} of the fecal pellet production, investigating the interactions between the 2 stressors at expected future conditions. We hypothesized that *C. glacialis*, being a species more closely associated with sea ice, will show higher tolerance to salinity extremes, but also that low salinity in combination with high temperatures might offer an advantage to the Atlantic species, *C. finmarchicus*.

2. MATERIALS AND METHODS

2.1. Experimental organisms

Sampling was conducted by local hunters in Disko Bay, near Qeqertarsuaq, approximately 0.5 nautical miles off the coast on 7 April 2021 (Fig. 1). *In situ* salinity and temperature were 33.5 and -1°C , respectively. The copepods *Calanus finmarchicus* and *C. glacialis* were collected using a WP-3 plankton net with a large non-filtering cod-end. The nets were hauled with a speed of 0.5 m s^{-1} , in the upper 50 m of the water column. On board, the content of the cod-end was emptied into a 70 l thermo-box with approximately 30 l of surface water and closed to avoid ice formation during transport to the laboratory. The samples were in the laboratory 1 h after collection. There, ap-

proximately 750 females of each species were sorted from the samples, using their size and red pigmentation of the antennas and somites as identification criteria (Nielsen et al. 2014). Sorting was conducted in a cold room (0°C) using a small, ice-chilled Petri dish, under a dissecting microscope.

2.2. Phytoplankton culture and experimental setup

Cultures of the diatom *Thalassiosira weissflogii* were grown in 5 l aerated glass jars. Surface seawater that was heated for 2 h to 60°C (to eliminate other organisms) was used for the cultures. Vitamin-enriched B_1 medium (1 ml l^{-1}) and 1 ml l^{-1} silicate ($500\text{ }\mu\text{M}$) were added daily (Hansen 1989). The cultures were diluted daily to keep them in an exponential growth phase. The cultures were grown at a 12:12 h light:dark cycle with $50\text{ }\mu\text{E m}^{-2}\text{ s}^{-1}$, at $20 \pm 2^{\circ}\text{C}$. The abundance of the cells in the cultures was measured daily; samples (2 ml) were fixed in acid Lugol's solution (1% final concentration). A 1 ml aliquot of the sample was then transferred to a Sedgewick Rafter Counting Chamber and enumerated under a microscope. The targeted carbon concentration estimated to correspond to saturating food levels was $400\text{ }\mu\text{g C l}^{-1}$ (Reigstad et al. 2005). To calculate the number of *T. weissflogii* cells corresponding to the necessary amount of carbon, a cellular carbon con-

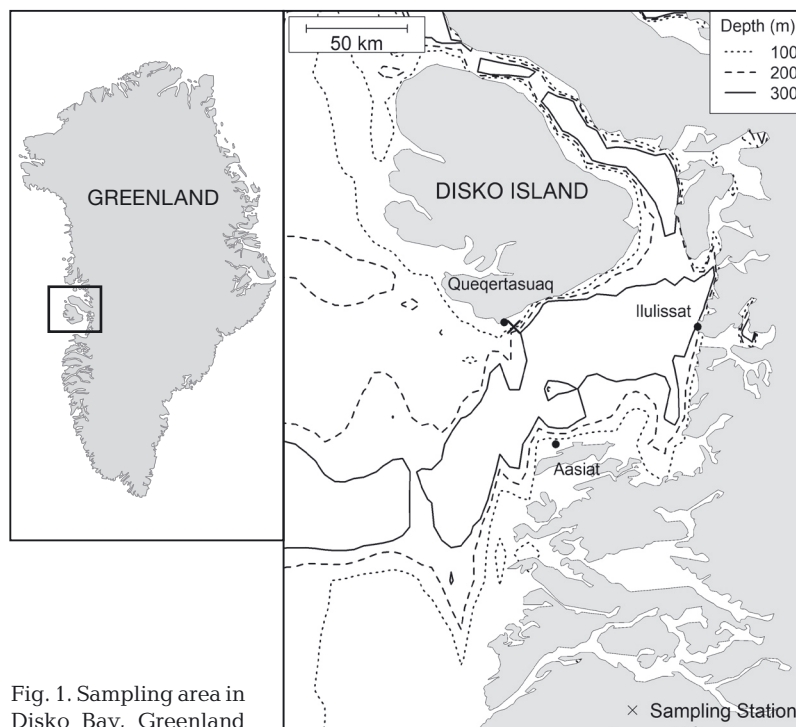


Fig. 1. Sampling area in Disko Bay, Greenland

tent value of $131 \text{ pg C cell}^{-1}$ was used (Dutz et al. 2008). Therefore, the targeted *T. weissflogii* cell concentration was $3035 \text{ cells ml}^{-1}$.

Two types of experiments were conducted to estimate mortality and fecal pellet production rates, respectively. The experimental setup covered 3 temperatures (0, 5 and 10°C) and 12 salinities, ranging from 5 to 60, in intervals of 5, excluding the *in situ* salinity of 33.5. Surface seawater with a salinity of 33.5 was used for all the experiments. The experiments were conducted in temperature-controlled containers, where the temperature was logged every 10 min using HOBO thermo-loggers (Table 1). Aquarium salt and fresh water from a nearby spring were used to increase and decrease the salinity, respectively. A hand-held Leiz refractometer was used for all salinity measurements and adjustments.

2.3. Mortality experiment

On the first day, 4 buckets with 5 l of surface seawater and a false bottom cylinder (28.3 cm high and 18 cm in diameter) with a $400 \mu\text{m}$ mesh were prepared.

Table 1. Temperature during the experiment, as recorded by the temperature loggers. Intended and measured temperature with standard deviation is presented

Intended temperature ($^\circ\text{C}$)	Measured temperature ($^\circ\text{C}$)
0	-0.08 ± 0.94
5	4.36 ± 0.67
10	9.72 ± 0.34

The experiment started with 2 buckets per species, at a salinity of 33.5, where they were left to acclimatize for 24 h. The next day, 4 new buckets were created, 2 with a salinity of 30 and 2 with a salinity of 35. The false bottom cylinders were gently transferred to new buckets of increased and reduced salinity, resulting in 2 buckets per species, 1 for each of the new salinities.

Every day, for 7 consecutive days, 4 new buckets were created, of increasing and decreasing salinities, and the animals were transferred. This process occurred at the intermediate temperature of 5°C . Daily food additions were made to sustain basic metabolic activity. Following each transfer, copepods were acclimatized for 24 h at the respective salinity, at 5°C . After the acclimatization, alive intact females were picked with a Pasteur pipette and transferred individually to 24-well tissue culture plates (NUNC™ Multi wells) containing 3 ml of seawater. The females were incubated in the 3 temperature-controlled rooms at 0, 5 and 10°C and at the respective salinity. The multi-well plates were examined daily using a dissecting microscope, and dead individuals were enumerated. The cumulative mortality was then estimated during this period. The total duration of the mortality experiment was 12 d (Fig. 2).

2.4. Fecal pellet experiments

After the mortality estimation, all surviving individuals from each treatment were transferred from the tissue culture trays to 1 l glass jars containing $400 \mu\text{g C ml}^{-1}$ of *T. weissflogii*. The copepods were left to acclimatize for 24 h, at saturating food conditions and at the 3 different temperatures, at the respective salinity. After the acclimatization, 12 individuals were ran-

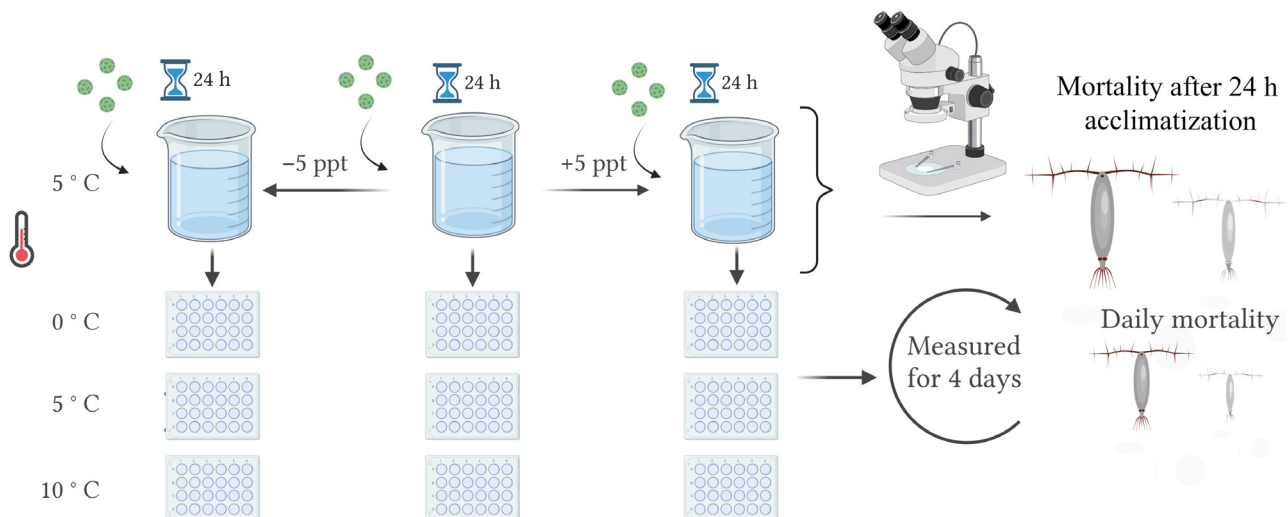


Fig. 2. Experimental setup for the estimation of mortality

domly selected and allocated into 3 replicate polycarbonate incubation bottles containing 1 l of seawater containing $400 \mu\text{g C l}^{-1}$ of *T. weissflogii*. The bottles were then incubated for 18–24 h and turned by hand every 6 h to keep the food in suspension. After incubation, the content of the bottles was filtered onto a $20 \mu\text{m}$ mesh, and females and pellets were enumerated under the dissecting microscope (Fig. 3).

Experiments have demonstrated that *C. finmarchicus* is mainly involved in coprorhexy, i.e. creates fragments of fecal pellets, while coprophagy, i.e. the ingestion of pellets, is rare (Noji et al. 1991). To avoid counting fragments of pellets, only pellets that were 3 times longer than their width were considered. Daily fecal pellet production (FPP) rates were then calculated (pellets female $^{-1}$ d $^{-1}$). Subsamples of 36 and 105 females of *C. glacialis* and *C. finmarchicus*, respectively, were fixed in acid Lugol's solution and the prosome length (PL, μm) was measured. In addition, 254 and 159 fecal pellets were fixed, respectively, and their length and width were measured. Their volume (V_{FP} , μm^3) was then calculated by assuming they have a cylindrical shape. To account for shrinkage of females and pellets after fixation with Lugol's solution, a shrinkage percentage of 16.5% was applied (Jaspers & Carstensen 2009). V_{FP} was converted to carbon (C_{FP} , $\mu\text{g C pellet}^{-1}$) using a carbon to pellet volume relationship of $C_{\text{FP}} = 4.3 \times 10^{-8} \times V_{\text{FP}}$ (Swalethorp et al. 2011). The following relationship was used to calculate female carbon content (C_{Fem}), as has been described for *Calanus* spp. in pre-bloom conditions: $C_{\text{Fem}} = 0.0018 \times \text{PL}^{4.1}$ (Swalethorp et al. 2011), where

PL is the prosome length. Specific fecal pellet production rate (SPP, $\mu\text{g C}_{\text{FP}} \mu\text{g C}_{\text{Fem}}^{-1} \text{d}^{-1}$) was calculated using the following equation: $\text{SPP} = \text{FPP} \times C_{\text{FP}}/C_{\text{Fem}}$, where FPP was estimated during the experiment, and C_{FP} is the fecal pellet carbon content

2.5. Q_{10} estimation

To estimate the thermal sensitivity of FPP of the 2 species and compare it to previous studies, we calculated the Q_{10} temperature coefficient. The Q_{10} values were calculated for 3 temperature intervals: 0–5, 5–10 and 0–10°C (Hirche & Bohrer 1987, Grote et al. 2015). Q_{10} calculations were done as follows:

$$Q_{10} = \frac{k_1}{k_2}^{10/(T_1 - T_2)} \quad (1)$$

where k_1 and k_2 are the FPP rates at temperatures T_1 and T_2 , respectively.

2.6. Statistical analysis

As the experiment was replicated with 24 animals per treatment, the resulting dataset consisted of daily counts of both dead and alive individuals (dead were denoted with 1 and alive with 0). For each species and treatment, a linear model was fitted to the cumulative daily counts of dead and alive individuals. (Table S1 in the Supplement at www.int-res.com/articles/suppl/m729p047_supp.pdf). The daily mortality rates were

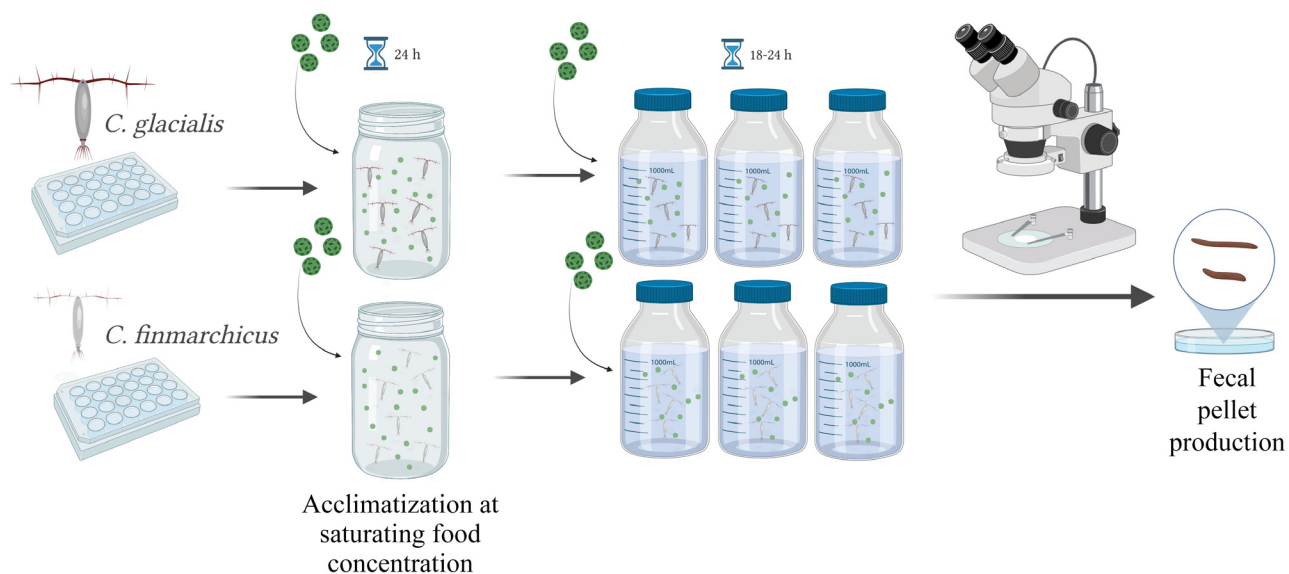


Fig. 3. Experimental setup for the estimation of fecal pellet production

calculated as the slopes of the fitted linear models. Mortality rates among treatments were compared by testing the overlap of the 95% confidence intervals of the estimated slopes.

For the estimation of 50% lethal concentrations (LC_{50}) for the 2 species with respect to temperature, we fit a second-degree polynomial equation to the cumulative mortality data at each day of the exposure period, according to David et al. (1997):

$$M = aS^2 + bS + c \quad (2)$$

where S is salinity, M is mortality, and a , b , c are the estimated polynomial parameters.

When the second-degree polynomial was not suitable for the data, we proceeded with a third-degree polynomial equation:

$$M = M_{ip} + k(S - S_{ip}) + g_3(S - S_{ip})^3 \quad (3)$$

where M_{ip} is the intercept, S_{ip} is salinity at the inflection point of the sigmoid function, and k and g_3 are polynomial parameters.

LC_{50} values were calculated by performing bootstrap resampling on the fitted non-linear models, generating 1000 bootstrap samples. Statistically significant differences between the estimated LC_{50} values of the curves among temperature treatments and among the 2 species at each temperature were calculated using 2-way ANOVA on the bootstrapped values ($\alpha = 0.05$), and post-hoc comparisons were done using Tukey's test ($\alpha = 0.05$). All statistical analyses were conducted using RStudio (R version 4.2.2).

For SPP, ANOVA ($\alpha = 0.05$) was performed to investigate whether there were significant differences in the mean SPP among the experimental groups. Different models were constructed to investigate differences across different salinities at each of the 3 temperatures. To make pairwise comparisons and investigate the statistical differences between SPP at control salinity and each salinity, post-hoc analysis, using Dunnett's T3 test ($\alpha = 0.05$) was performed. No violations of the initial model assumptions were observed.

3. RESULTS

3.1. Mortality

The cumulative mortality increased over the 96 h of the experiment for each treatment (Fig. 4). The linear models fitted to the mortality data as a function of the exposure time can be seen in Figs. S1 & S2 in the Supplement. The coefficients of the linear models fitted to the data are provided in Tables A1 & A2 in the

Appendix. The resulting survival rates show a dome-shaped response to salinity for both *Calanus finmarchicus* (Fig. 5a) and *C. glacialis* (Fig. 5b)

Differences in mortality rates among species and treatments were assessed by evaluating the overlap of the 95% confidence intervals (Table S1), providing a measure to discern significant distinctions in the observed effects. In conditions of salinity below 15, the 2 species exhibited distinct responses, particularly evident in the significantly higher mortality rates of *Calanus finmarchicus* at temperatures 0 and 10°C, where there was no overlap in the 95% confidence intervals. However, at the intermediate temperature, differences among species were discernible only at a salinity level of 10 (Fig. 5; Table S1). Under extremely saline conditions, the 2 species did not demonstrate significant differences in their daily mortality rates. At 0°C, *C. finmarchicus* showed an increase in its mortality rate at the shift in salinity from 20 to 15 (from 0.01 to 0.08), increasing sharply to 0.5 during the shift in salinity from 15 to 10. In contrast, *C. glacialis* showed no increase in mortality at a salinity of 15 and a mortality of 0.1 at a salinity of 10, at the same temperature. *C. glacialis* showed a difference in its response with increased temperature, reaching a mortality of 0.19 at a salinity of 10.

To estimate LC_{50} , a polynomial equation was fitted to the mortality data (Fig. 6). A third-degree polynomial was fitted to the data for 5°C, at salinities below control, while for the rest of the treatments, a second-degree equation fitted the relationship between mortality and salinity (Fig. 6c,d, Tables A2 & A3). At salinities below 33, temperature (ANOVA, $F_{2,5994} = 9305$, $p < 0.0001$), species (ANOVA, $F_{1,5994} = 139060$, $p < 0.0001$) and their interaction (ANOVA, $F_{2,5994} = 2003$, $p < 0.0001$) were significant in explaining differences in LC_{50} values.

The LC_{50} for *C. finmarchicus* at 96 h of exposure was estimated to be 14 ± 0.35 at 0°C (mean \pm SE), decreasing to 13.5 ± 0.59 at 5°C and then increasing to 14.6 ± 0.55 at 10°C ($p < 0.0001$) (Table 2). For *C. glacialis*, the LC_{50} at 96 h at the low salinities at the 3 respective temperatures was 9 ± 1.98 , decreasing, although not significantly, to 8.5 ± 0.94 and increasing to 11.2 ± 0.68 , respectively ($p < 0.001$) (Table 2). *C. finmarchicus* had significantly lower LC_{50} than *C. glacialis* at all temperatures tested. The LC_{50} values at each temperature and exposure time can be seen in Fig. 7.

At the salinity range above 33, at 96 h of exposure, *C. finmarchicus* had an LC_{50} of 59.2 ± 0.42 at the lowest temperature, decreasing to 57 ± 0.35 at the intermediate temperature and decreasing again to 55 ± 0.45 at 10°C (Table S2). No statistically significant differences

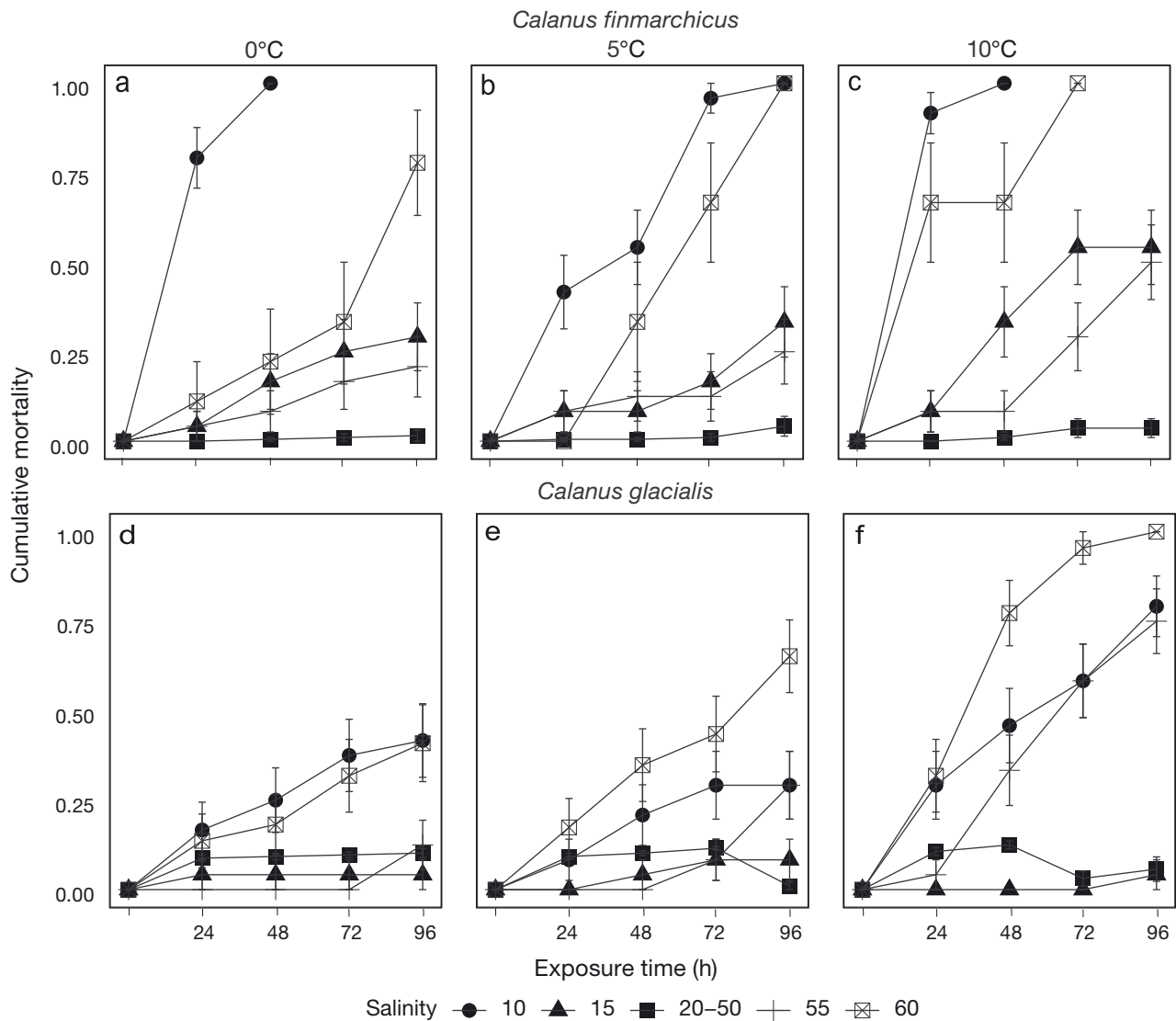


Fig. 4. Cumulative mortality (mean with standard error) of (a–c) *Calanus finmarchicus* and (d–f) *C. glacialis* over 96 h exposure at different salinities and temperatures

were observed in the LC_{50} of *C. finmarchicus* among the different temperatures. *C. glacialis* had an LC_{50} of 63.6 ± 2.95 , 58.3 ± 1.23 , and 53.3 ± 0.55 at each of the 3 respective temperatures at 96 h of exposure (Table S2), but no statistically significant differences were observed among the different temperatures. No statistically significant differences between the LC_{50} of the 2 species were observed at high salinities.

3.2. SPP and Q_{10}

Significant differences in SPP across salinities were found for both *C. finmarchicus* (ANOVA, $F_{9,78}$, $p < 0.0001$) and *C. glacialis* (ANOVA, $F_{11,91}$, $p < 0.0001$).

For *C. finmarchicus* at all temperatures, SPP decreased significantly at salinities below 15 and above 50, while increases in SPP were observed at a salinity of 20 at 0°C, and at 10°C at a salinity of 25, while there were no differences in SPP between salinities of 25 and 40 (Table A1, Fig. 8).

For *C. glacialis*, at 0 and 5°C, a significant decrease in SPP was observed at salinities over 50, but not at the salinity of 15, as with *C. finmarchicus*. An increase in SPP was also observed at a salinity of 20 for this species, at the lowest temperature (Table A1). At 10°C, a significant decrease in SPP from the control was only observed at a salinity of 55 (-0.02 , $p < 0.001$), while significant increases were observed at the low salinities of 20 and 15 (Table A1).

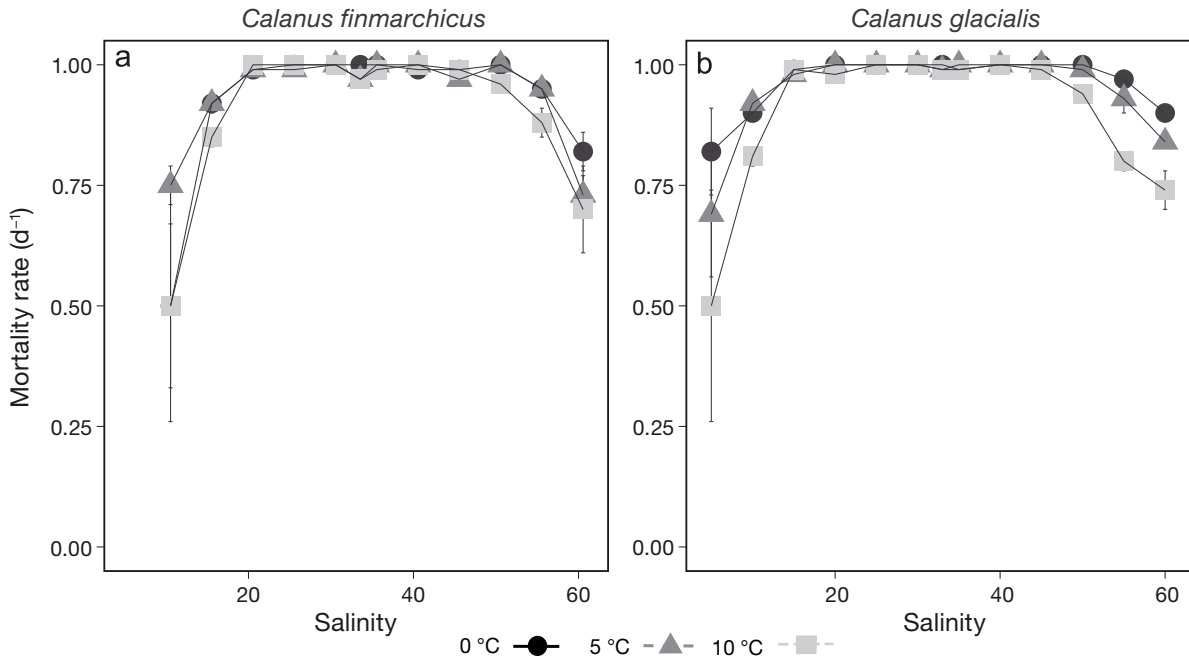


Fig. 5. Daily survival rate (mean with standard error) for (a) *Calanus finmarchicus* and (b) *C. glacialis*

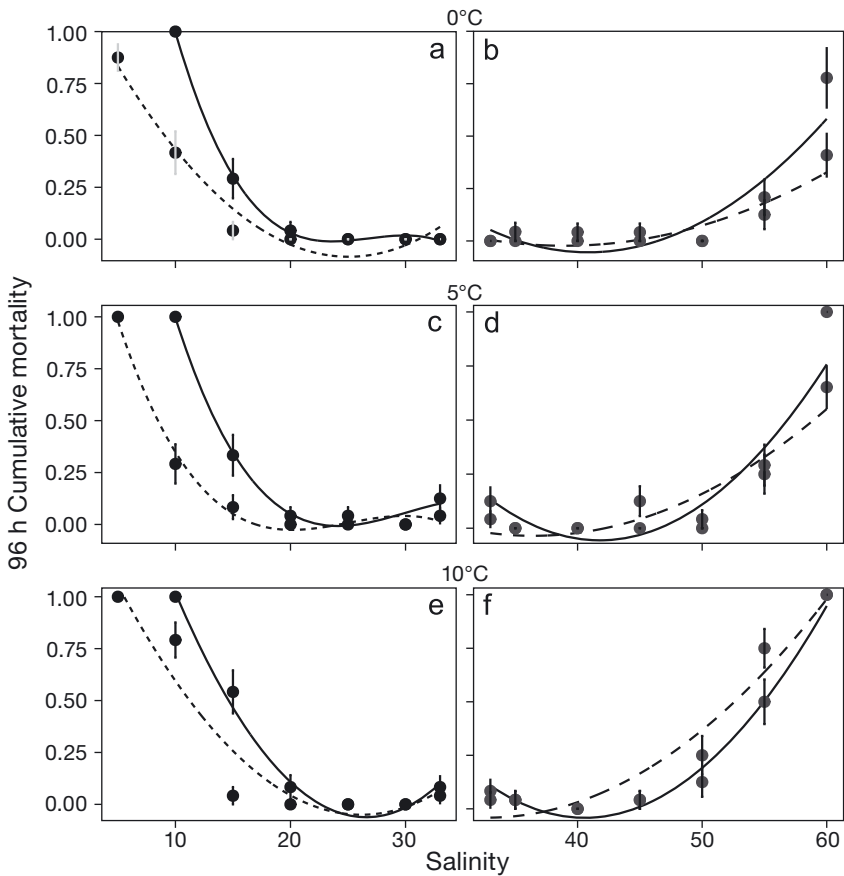


Fig. 6. Cumulative mortality (mean with standard error) and fitted curves for the 2 species at each temperature and salinity range. *Calanus finmarchicus* is represented with a solid line, *C. glacialis* with a dashed line

SPP for *C. finmarchicus* increased with temperature for the salinity range within 25–40 (Fig. 9), with a Q_{10} that ranged from 0.9 to 2.6 (Table 3). Outside of that range of salinities, this relationship was not apparent, and the Q_{10} values exceeded that range (Table 3). For *C. glacialis*, the SPP increased between 0 and 5°C with a Q_{10} between 2.2 and 2.4 for the salinity range of 20–45 (Table 3, Fig. 9). For the temperature interval between 5 and 10°C, FPP decreased for all salinities in this range, except for 40 (Fig. 9). The Q_{10} in that interval ranged between 0.3 and 0.7 (Table 3). For the more extreme salinities, no relationship between SPP and temperature was found.

4. DISCUSSION

In the present study, ranges of salinity tolerance, defined by the cumulative mortality at 96 h of exposure, were significantly broader for *Calanus glacialis* towards low salinities, while both species had broad tolerance to high salinities. In previous work, long-term exposure to increased salinities led to 100% mortality after 20 d at a

Table 2. Salinity LC₅₀ values with 95% confidence intervals (95% CI) and p-values at 96 h of exposure computed from the fitted model

Salinity	Temperature (°C)	LC ₅₀	95% CI	p
<i>Calanus finmarchicus</i>				
5–33	0	14	13.3–14.7	0.462
	5	13.5	12.6–14.7	0.508
	10	14.6	13.9–15.4	0.472
33–60	0	59.2	56.6–64.2	1
	5	57	55.6–59	0.511
	10	55	53.8–56.4	0.497
<i>Calanus glacialis</i>				
5–33	0	9	7.8–10	0.504
	5	8.5	7.8–9.4	0.46
	10	11.2	10.3–12.2	0
33–60	0	63.6	59.6–70.8	0.535
	5	58.3	56.4–61.1	0.496
	10	53.3	52.2–54.3	0.483

salinity of 40 and 10 d at a salinity of 50 (Grainger & Mohammed 1990). Even though the long-term effects of exposure to high salinities differ from the present study, our results point towards a short-term acclimation to a wide range of salinities, by far wider than what is experienced by pelagic copepods at high latitudes, where salinities typically only vary between 31 and 34 (Hansen et al. 2012).

The potential niche of the 2 species, as indicated by their FPP rates was between the salinities of 25 and 40. At salinities marginally exceeding this range (i.e. salinities of 20 at the low end and 45 at the high end), the FPP increased significantly from the control, providing evidence of energy-demanding osmoregulatory processes. Osmoregulation is a highly energy-demanding process and is therefore a strategy mostly adopted by organisms that regularly deal with extreme salinity fluctuations, such as the euryhaline copepod *Eurytemora affinis* (Roddie et al. 1984). Experiments on *E. affinis* have demonstrated increased metabolic demand under saturated food concentration when exposed to unfavorable salinity conditions (Hammock et al. 2016). Most pelagic crustaceans, however, including calanoid copepods, which are adapted to relatively stable salinity conditions, are considered osmoconformers (Charmantier 1998).

Non-essential free amino acids (FAAs) are the most common organic osmolytes used by osmoconformers (Yancey et al. 1982). This mechanism of volume regulation has also been observed in *C. finmarchicus* (Cowey & Corner 1963). Although *Tigriopus californicus* is a rock pool copepod, and thus, not directly comparable to pelagic copepods like *Calanus*, their ener-

getic expenditure of an increase in the concentration of FAAs, going through hyperosmotic shock (from 50 to 100% seawater), has been estimated at 11.6% of their daily energy needs (Goolish & Burton 1989).

Our results demonstrated an increase in egestion rates under osmotically stressful conditions. The salinity for optimal survival and adaptation of *Acartia tonsa* nauplii and adults has previously been estimated to be between 15 and 22 (Cervetto et al. 1999). Experiments on the metabolic balance of adults have shown increased FPP under extreme salinity conditions (salinities of 2 and 33) (Calliari et al. 2006), and reduced egg production, without a subsequent increase in ingestion rates, leading to a significant decrease in gross growth efficiency. This change in metabolic balance could be an indication of differences in the allocation of the ingested energy towards osmoregulatory processes. Moreover, *A. tonsa* individuals from the Caspian Sea, adapted to a salinity of 13, showed a significant increase in FPP when transferred to salinities of 20 and 35, with a decrease again at the extreme salinity of 45 (Shayegan et al. 2016).

To estimate the energetic cost of osmotic stress in the 2 *Calanus* species, further bioenergetic experiments are necessary. Our findings indicate both a higher energy expenditure with higher ingestion rates accompanied by higher egestion but could also be the manifestation of a lower assimilation efficiency of the ingested food, as part of a stress response. To make some inference regarding the strategies of the 2 *Calanus* species to cope with shifts in salinity, a specific study of the ionic composition or the concentration of free amino acids in the extracellular fluid of the 2 copepods should be conducted.

4.1. Low salinity extremes and their effects on *Calanus* spp.

The LC₅₀ of *C. glacialis* was significantly lower at low salinities than that of *C. finmarchicus*. Early work on the physiological plasticity of *C. finmarchicus* indicated the ability for short-term acclimatization to salinities as low as 12 (Marshall et al. 1935). In a recent study in the White Sea, *C. glacialis* adapted to a local salinity of approximately 26, and only minor mortality rates were found at salinities as low as 15 (Martynova & Ivankovich 2020). The effects on survival were prominent at salinities below 10; therefore, we suggest that *C. glacialis* will feed close to, but not directly underneath, the sea ice when melting is intense.

Later in spring, as the melting progresses, the coastal zones receive meltwater from glaciers and rivers.

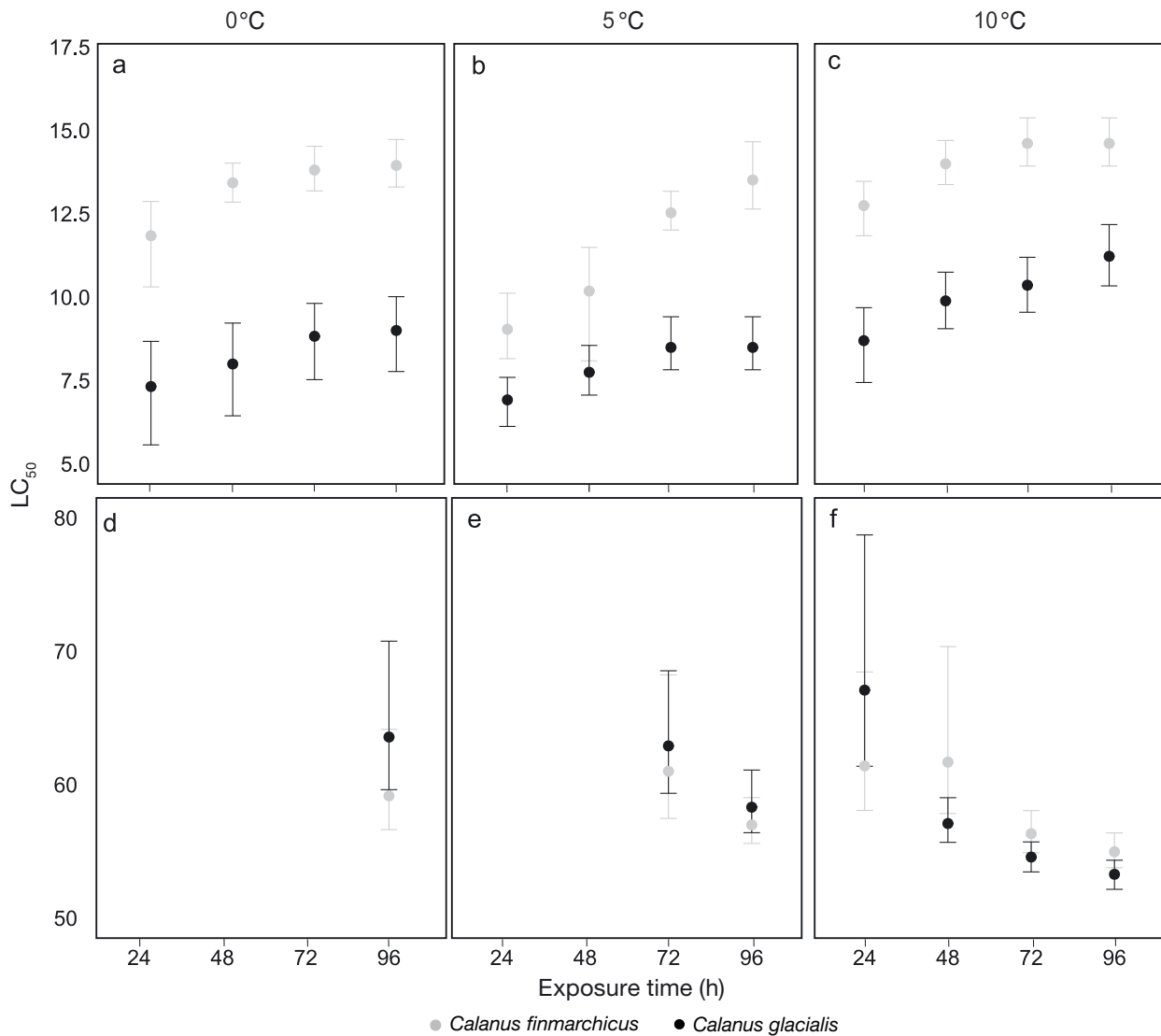


Fig. 7. Salinity lethal concentration (LC₅₀) values, with 95% confidence intervals, of the 2 species at different temperatures

As the season progresses, a warm and relatively fresh layer is formed at the surface, where temperatures can range from 5 to 13°C and salinities are between 15 and 20 (Tang et al. 2011b, Riisgaard et al. 2014). The chlorophyll maximum is found subsurface below the freshwater-influenced surface layer (Riisgaard et al. 2014, Middelbo et al. 2018). Various processes, such as upwelling near terminating glaciers, could lead to an accidental upwelling of *Calanus* spp. into low-salinity and low-temperature waters (Wesławski & Legeżyńska 1998). Moreover, the 'escape jumps' performed during swimming and feeding (Kiørboe et al. 2010) could lead to *Calanus* spp. being trapped for a specific period in the surface fresh and warm, stratified layer. Our results suggest that *C. finmarchicus* will be more sensitive than *C. glacialis* to salinities lower than 15.

4.2. High salinity extremes and their effects on *Calanus* spp.

The results from this study demonstrate high tolerance of both species to extreme salinities, with *C. glacialis* maintaining better condition under such circumstances. Other studies, with a less gradual shift in salinity, have shown very low survival of *C. glacialis* at salinities of 60 in contrast to under-ice copepods such as *Tisbe furcata*, which has better tolerance of extreme salinities of 60 and 70 (Grainger & Mohammed 1990). Our results show that *C. glacialis* can temporarily tolerate extremely high salinities at the water–ice interface where they are often found. The euryhalinity of *C. glacialis* was also confirmed by the fact that FPP was observed at the maximum salinities of 55 and 60 after they had survived for 5 d at those extremes. The mechanisms

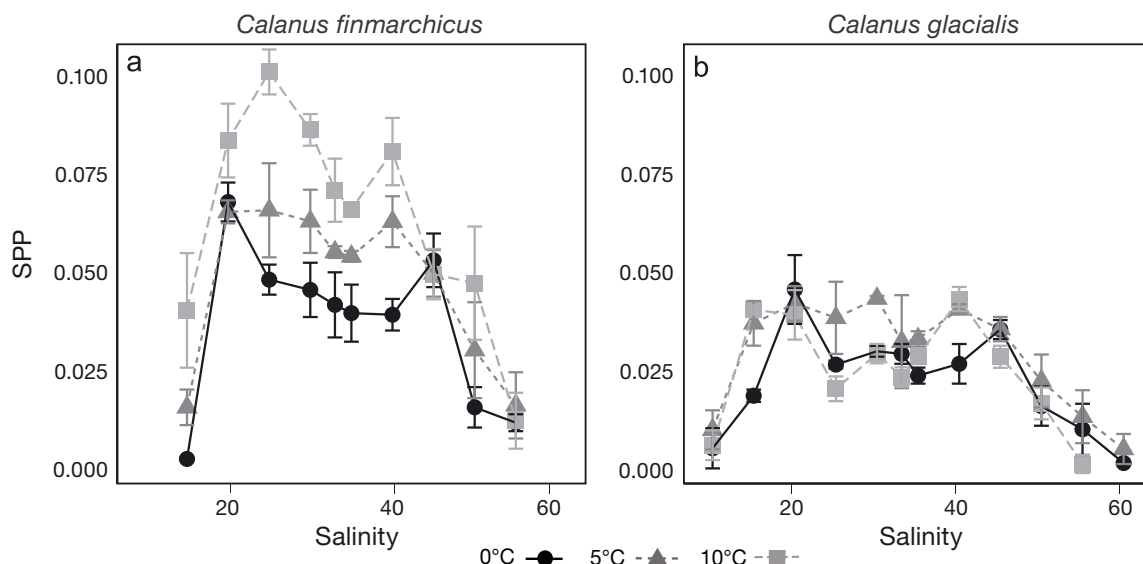


Fig. 8. Specific fecal pellet production (SPP, in $\mu\text{g C}_{\text{FP}} \mu\text{g C}_{\text{Fem}}^{-1} \text{d}^{-1}$; FP: fecal pellets; Fem: female) for (a) *Calanus finmarchicus* and (b) *C. glacialis* with standard deviation at different salinities, at the 3 temperatures

behind this ability in *C. glacialis* are unclear; lipid content may play a role in efficient osmoregulation. Copepods with high lipid content have been found to accumulate amino acids with higher molecular weight, like proline, compared to low-lipid copepods, which accumulate mostly alanine (Goolish & Burton 1989).

4.3. Temperature responses of *Calanus* spp.

Temperature-mediated mortality became apparent for both species only when exceeding their salinity tolerance window. The synergistic effects of the 2 stressors were more apparent at low salinity extremes for *C. finmarchicus* compared to *C. glacialis*, while the opposite result was observed at the high end of the salinity spectrum. SPP increased exponentially with temperature, at salinities inside the tolerance window for *C. finmarchicus*. The Q_{10} values are comparable with a range of Q_{10} values for FPP reported to be between 2 and 4 for *C. finmarchicus* (Kjellerup et al. 2012). The Q_{10} of the FPP rate increased with salinity approaching the extremes. The increase in Q_{10} values at salinity extremes is indicative of a synergistic interaction between the 2 stressors, which leads to increased thermal sensitivity for both *Calanus* species under intense freshening scenarios.

Inside the salinity tolerance window of *C. glacialis*, FPP increased between 0 and 5°C, decreasing again at higher temperatures. This thermal response follows Shelford's law of tolerance (Shelford 1913) around an optimum of 5°C. This response is in accordance with the response of *C. glacialis* egestion rates to tempera-

Table 3. Q_{10} values of fecal pellet production at different salinities

Temperature (°C)	Salinity	Q_{10}	
		<i>Calanus finmarchicus</i>	<i>C. glacialis</i>
0–5	10		1.4
	15		5.1
	20	0.9	0.9
	25	1.9	0.8
	30	1.9	1.0
	33	1.8	0.8
	35	1.9	1.2
	40	2.6	1.6
	45	0.9	0.8
	50	4.0	1.0
	55	2.0	0.2
5–10	10		4.7
	15		4.2
	20	1.6	0.8
	25	2.4	2.2
	30	1.9	2.2
	33	1.7	2.0
	35	1.5	2.0
	40	1.7	2.4
	45	1.0	1.0
	50	3.7	2.1
	55	0.6	1.9
0–10	10		0.3
	15		1.2
	20	1.2	0.9
	25	2.1	0.3
	30	1.9	0.4
	33	1.7	0.3
	35	1.7	0.7
	40	2.1	1.1
	45	0.9	0.6
	50	3.9	0.5
	55	1.1	0.0

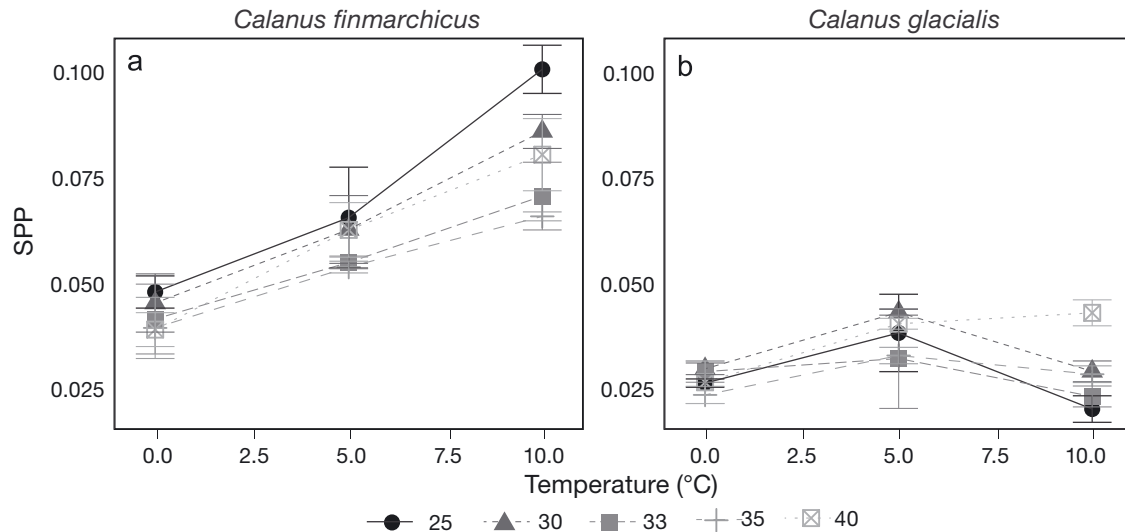


Fig. 9. Specific fecal pellet production (SPP, in $\mu\text{g C}_{\text{FP}} \mu\text{g C}_{\text{Fem}}^{-1} \text{d}^{-1}$; FP: fecal pellets; Fem: female) for (a) *Calanus finmarchicus* and (b) *C. glacialis* with standard deviation at each temperature, for salinities between 25 and 40

ture previously identified for the same area, but with Q_{10} values around 2, lower than the Q_{10} of 3–4 reported for *C. glacialis* during the spring bloom (Kjellerup et al. 2012). Linear increases in ingestion and fecal pellet production rates have been observed for *C. glacialis* stage V copepodites (CV) in Advent Fjord, Svalbard, during summer, over the same temperature range as in this study (Grote et al. 2015). In contrast, *C. glacialis* CV in the central Barents Sea in June fed optimally at 2.5 $^{\circ}\text{C}$ (Alcaraz et al. 2014). Comparisons between different populations should therefore be made with caution. Marine ectotherms can thermally acclimatize both seasonally and in a latitudinal cline (Pörtner 2001), which is achieved through the increase in mitochondrial density, to avoid temperature-induced hypoxia (Peck 2002).

Temperature affects other aspects of fitness, recruitment and ecological success of *Calanus* spp. in the Arctic. The metabolic balance of *C. glacialis*, estimated as the difference between ingestion and respiration, has been estimated to linearly decrease with temperature, reaching negative values when temperature exceeds 6 $^{\circ}\text{C}$ (Alcaraz et al. 2014). The comparative effect of temperature on the physiology and development of the 2 *Calanus* species has led to the identification of a threshold of 5–6 $^{\circ}\text{C}$, above which *C. finmarchicus* performs better than *C. glacialis* (Kjellerup et al. 2012, Pasternak et al. 2013, Jung-Madsen & Nielsen 2015).

4.4. Future changes in Arctic ecosystems

Our findings show the capacity of both species to cope with a wide range of salinities and temperatures.

Our study confirmed that *C. glacialis* can tolerate conditions close to the sea ice, where previous studies have established its nutritional dependence on ice algal blooms to initiate spawning in spring (Søreide et al. 2010, Durbin & Casas 2014).

In coastal west Greenland, a longer ice-free period is expected to lead to an earlier and more intense phytoplankton bloom followed by an intense summer protozooplankton bloom (Levinsen & Nielsen 2002, Michel et al. 2012). An earlier initiation and sedimentation of the ice algal bloom is also predicted (Leu et al. 2015). The comparative responses of the 2 species to an early phytoplankton bloom were discussed by Kjellerup et al. (2012). The inability to refuel lipid reserves used for overwintering in *C. glacialis* was observed in an early-bloom scenario (Kjellerup et al. 2012). The decreases in gonad maturation with increased temperatures observed could favor *C. finmarchicus* to be ready for an early phytoplankton bloom under increased temperatures (Niehoff et al. 2002). An increase in the ice-algal bloom, according to our findings, would be favorable for *C. glacialis*, which tolerate the extreme salinity fluctuations next to the sea-ice during spring. In the short term, the effects of environmental changes will have an effect of phenological plasticity of the *Calanus* spp. Genetically driven evolutionary processes may modify the comparative responses of the 2 species under different scenarios. *C. finmarchicus* has a shorter life cycle than *C. glacialis*, which might lead to a faster adaptation to future conditions in areas of co-occurrence of the 2 *Calanus* species. In the intertidal copepod *T. californicus*, rapid selection after only 5 generations of exposure to osmotic stress has been observed (Kelly et

al. 2016). However, one of the effects of temperature rises and earlier blooms in the Arctic will probably be a shift in the *C. glacialis* life cycle from 2 to 1 yr (Møller & Nielsen 2019), which deprives *C. finmarchicus* of this evolutionary advantage.

4.5. Conclusion

Our results demonstrate the euryhalinity of both *Calanus* species, with *C. glacialis* being more tolerant to extreme salinities, showing lower mortality and better condition. Our study, in combination with previous work, established that *C. glacialis* can exploit the spring algal bloom to fuel its lipid reserves and initiate spawning. A climate change scenario with an earlier sea-ice breakup, and therefore initiation of the phytoplankton bloom, might constitute an advantage for *C. glacialis*, whose gonads mature earlier in spring. However, a temperature increase might accelerate gonad maturation for *C. finmarchicus*, causing *C. glacialis* to lose its advantage of early spawning. A potential freshening of the surface layer in spring, with more frequent events of glacial meltwater intrusion, will increase the possibility of *Calanus* encountering such conditions, when feeding underneath that layer. According to our results, *C. glacialis* is more capable of tolerating such short-term encounters with extremely low salinities. To estimate the energetic cost of coping with osmotic stress, we suggest that further bioenergetic calculations are necessary.

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Appendix.

Table A1. Second-degree polynomial model coefficients for 96 h mortality (see Eq. 2)

Salinity	Temperature (°C)	Species	$a \pm SE$	$b \pm SE$	$c \pm SE$
<33	0	<i>Calanus finmarchicus</i>	0.004 ± 0	-0.127 ± 0.009	4.229 ± 0.714
	0	<i>Calanus glacialis</i>	0 ± 0	-0.116 ± 0.024	2.558 ± 0.15
	10		0.004 ± 0	-0.067 ± 0.024	3.091 ± 0.625
>33	0	<i>Calanus finmarchicus</i>	0.001 ± 0	-0.209 ± 0.017	2.84 ± 0.611
	10		0.001 ± 0	-0.079 ± 0.018	2.716 ± 0.167
	5		0.002 ± 0	-0.199 ± 0.033	2.076 ± 0.545
	5	<i>Calanus glacialis</i>	0.002 ± 0	-0.114 ± 0.01	4.275 ± 0.739
	0		0.001 ± 0	-0.182 ± 0.026	1.348 ± 0.082
	10		0.003 ± 0	-0.134 ± 0.026	3.375 ± 0.632

Table A2. Third-degree polynomial model coefficients for 96 h mortality (see Eq. 3)

Salinity	Temperature (°C)	Species	$M_{ip} \pm SE$	$k \pm SE$	$S_{ip} \pm SE$	$g_3 \pm SE$
<33	5	<i>Calanus finmarchicus</i>	0.056 ± 0.055	0.016 ± 0.011	29.987 ± 4.034	0 ± 0
<33	5	<i>Calanus glacialis</i>	0.008 ± 0.023	0.01 ± 0.003	24.99 ± 1.371	0 ± 0

Table A3. Dunnett's *t*-test results for specific fecal pellet production. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Temperature	Salinity	Difference		p	
		<i>Calanus finmarchicus</i>	<i>C. glacialis</i>	<i>C. finmarchicus</i>	<i>C. glacialis</i>
0	15–33	-0.03912	-0.01062	2.1×10^{-5} ***	0.1367
	20–33	0.026149	0.016348	0.00093 ***	0.0089 **
	25–33	0.006399	-0.00272	0.80997	0.993
	30–33	0.003817	0.000666	0.98567	1
	35–33	-0.00205	-0.00552	0.99984	0.7477
	40–33	-0.00244	-0.00252	0.99937	0.9958
	45–33	0.0113339	0.00619	0.26072	0.6422
	50–33	-0.02602	-0.01324	0.00095 ***	0.0413 *
	55–33	-0.02987	-0.01915	0.00016 ***	0.0020 **
5	15–33	-0.03939	-0.0042	7.2×10^{-5} ***	0.9875
	20–33	0.010214	0.000861	0.5273	1
	25–33	0.010573	-0.00281	0.4906	0.9992
	30–33	0.007788	0.002425	0.783	0.9998
	35–33	-0.00112	-0.00816	1	0.709
	40–33	0.007705	-0.00063	0.791	1
	45–33	-0.00536	-0.00567	0.9592	0.9323
	50–33	-0.02493	-0.01883	0.0167 *	0.0399 *
	55–33	-0.03891	-0.0279	4.1×10^{-5} ***	0.0014 **
10	15–33	-0.03042	0.017071	0.0350 *	0.00031 ***
	20–33	0.012601	0.01578	0.6245	0.00076 ***
	25–33	0.029993	-0.00298	0.0178 *	0.93291
	30–33	0.015311	0.005943	0.4211	0.37824
	35–33	-0.00474	0.005265	0.9973	0.50508
	40–33	0.009885	0.019791	0.8297	3.3×10^{-5} ***
	45–33	-0.02126	0.005149	0.1358	0.52875
	50–33	-0.02356	-0.0067	0.0820	0.26306
	55–33	-0.05843	-0.02047	8.8×10^{-6} ***	1.9×10^{-5}