Calanus finmarchicus egg production at its northern border

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How the distribution of *Calanus finmarchicus* and its potential northward expansion will be affected by climate changes depends on the mechanisms and processes constraining their reproduction, recruitment and survival. Here we present measurements of *C. finmarchicus* egg production rates during the spring bloom in 2008, 2010 and 2011 in Disko Bay, West Greenland and validate four independently derived metabolic models to predict egg production rates. The spring bloom in 2008 was short and intense and supported lower cumulated specific egg production of *C. finmarchicus* than the longer blooms with lower peak biomass in 2011 and 2012. The models predicted different timing of initialization and development of egg production rates based on phytoplankton biomass and temperature and model performance varied from 'poor' to 'very good'. Phytoplankton biomass controlled the changes in egg production rates during the spring in Disko Bay, while the low temperature in the Bay explained why the egg production rate here is much lower than at more southerly localities despite high food concentrations. This study suggests that an increase in magnitude of the Arctic phytoplankton spring bloom will not result in increased copepod egg production, whereas a longer bloom and increasing temperatures will.

KEYWORDS: *Calanus finmarchicus*; plankton; distribution; phenology; egg production

INTRODUCTION

The copepod *Calanus finmarchicus* is a key species in the North Atlantic, but also inhabits Arctic areas (Hirche and Kosobokova, 2007; Swalethorp *et al.*, 2011; Beaugrand *et al.*, 2013). It is an important prey for many species of fish (Gaard and Reinert, 2002; Gislason and Astthorsson, 2002; Ringuette *et al.*, 2002), and it has been suggested that changes in its standing stock are responsible for variations in the cod stock (Beaugrand *et al.*, 2003). The center of distribution is the North Atlantic subarctic gyre, although a northward extension of the species has been associated with increasing

temperatures (Beaugrand *et al.*, 2013). How far north *C. finmarchicus* can spread in the future depends on the mechanisms and processes constraining their reproduction, recruitment and survival.

To understand how pelagic ecosystems will change in the future, knowledge about how climate-mediated changes will propagate through the food chain is essential. *C. finmarchicus* is an income breeder (Runge and Plourde, 1996; Varpe *et al.*, 2009), i.e. eggs are produced based on what they consume, in contrast to capital breeders that depend on stored energy for egg production. Thus, for *C. finmarchicus* we expect a strong link between food availability and egg production. Generally, the grazing rate of copepods is influenced by temperature, food concentration and body size (Saiz and Calbet, 2007), as well as by turbulence, prey type and size and predator avoidance (Saiz and Kiørboe, 1995; Titelman and Kiørboe, 2003). Temperature and food concentration are routinely measured during monitoring of marine ecosystems, whereas the latter are more difficult to obtain.

Here we investigate the egg production rates of *C. finmarchicus* at the northern part of its distribution in Disko Bay (Western Greenland), during the spring phytoplankton bloom in 3 different years. We then examine how the egg production rate during the phytoplankton spring bloom can be predicted from routine monitoring parameters like temperature and food concentration (Chlorophyll *a*) tested for four different versions of a model developed for *C. finmarchicus* previously applied to the North Sea (Møller *et al.*, 2012; Maar *et al.*, 2013).

METHOD

Measurements of egg production rate in Disko Bay

The seasonal succession of temperature, salinity, ice cover, phytoplankton (in terms of Chl *a* and fluorescence) and egg production rates of *C. finmarchicus* were measured in Disko Bay, western Greenland, at a 300 m deep monitoring station (69° 14N, 53° 23W) in 2008, 2011 and 2012. Data from 2008 on these variables and female individual biomass were published in Swalethorp *et al.* (2011).

From March to May, sampling was carried out once a week; during the phytoplankton spring bloom sampling was intensified to every 2–5 days. Before the break-up of sea ice, sampling was carried out through a hole in the ice at approximately the same location depending on ice conditions, and after sea ice break-up from the R/V Porsild (Arctic station, Copenhagen

University). Salinity, temperature and fluorescence were measured with a Seabird CTD (SBE25-01). Data on sea ice coverage was provided by the Copenhagen University Arctic Station monitoring program (Hansen *et al.*, 2006). Seawater samples to measure Chl *a* concentration were collected at 1, 20 and 50 m, and at the depth of the fluorescence maximum using Niskin bottles. Total Chl *a* was determined by filtratering 100–250 mL of seawater in triplicate per depth onto GF/F filters. In addition, at 1 m, the fluorescence maximum and 50 m, extra triplicates were filtered onto 10-μm filters. Filters were extracted in 5 mL 96% ethanol for 24 h (Jespersen and Christoffersen, 1987) and measured fluorometrically before and after acidification on a Turner fluorometer (TD-700) calibrated against a Chl *a* standard. Chl *a* was averaged in 0–50 m after a trapezoid integration.

C. finmarchicus females were sampled in the upper 100 m using a 200 μm mesh size WP-2 net with a large non-filtering cod-end. After sampling, copepods were quickly transferred to buckets submerged in thermo-boxes filled with seawater. Within 2–4 h of collection adult females were sorted in Petri dishes kept in ice-filled trays under a dissecting microscope and 15–20 females were incubated individually in 600 mL polycarbonate bottles. The bottles were filled with 45-μm screened sea water from the depth of maximum fluorescence, and incubated in thermos-boxes filled with ice and water. Temperature was kept at 0°C by addition of ice, and the temperature was logged every 15 min. After incubation (~48 h) the content of the bottles were filtered onto a 45-μm filter, eggs were counted and female length recorded. The egg production rate (EP, egg female^{-1} d^{-1}) and specific egg production rate (SEP, μgC μgC female^{-1} d^{-1}) was calculated assuming a carbon egg content of 0.21 μg C, and using a copepod C-weight to length regression based on measurements carried out in 2008 (Swalethorp *et al.*, 2011).

Prediction of grazing and egg production

Grazing expressed as weight-specific ingestion [g_i (μgC prey) (μgC copepod)$^{-1}$ d^{-1}] is predicted by maximum weight-specific ingestion (I_{max} (μgC prey) (μgC copepod)$^{-1}$ d^{-1}), and the dependency of ingestion on temperature ($f1$) and availability of food ($f2$):

$$g_i = I_{max} \cdot f1 \cdot f2 \qquad (1)$$

Thus, the functions $f1$ and $f2$ (ratios from 0 to 1) express how much I_{max} is reduced due to sub-optimal temperature and food conditions, respectively.

The response of ingestion rates to temperature (T, in Celsius) was described by a parabolic threshold function (Kooijman, 2000), where P_1 and P_2 are the lower and

upper boundaries of the tolerance range, and P_3 and P_4 are the Arrhenius temperatures for the rate of the decrease at both respective boundaries. P_5 is a coefficient applied after the fitting procedure to set the maximum to 1.

$$f1 = \frac{P_5}{\left(1 + \exp\left(\frac{P_3}{T - 273.15} - \frac{P_3}{P_1}\right) + \exp\left(\frac{P_4}{P_2} - \frac{P_4}{T - 273.15}\right)\right)} \quad (2)$$

Parameter values for the model have been described and validated previously for *C. finmarchicus* (Table I). The temperature in our incubations was held constant at 0°C, and *f1* was therefore 0.21 in all cases (Møller *et al.*, 2012).

The dependency of ingestion on food concentration (F, μg Chl a L^{-1}) is described by a Type 3 functional response (Gentleman and Neuheimer, 2008):

$$f2 = \frac{F^2}{(F^2 + K_m^2)} \quad (3)$$

where K_m (μg Chl a L^{-1}) is the half saturation coefficient.

Predictions of specific egg production rate (SEP, d^{-1}) were tested for four different models (Table II) based on the grazing estimate in equation 1 and estimated as follows:

$$SEP = g_i \cdot AE \cdot (1 - R_a) \cdot P_{egg} \quad (4)$$

where R_a (μgC$_{resp}$ μgC$_{ingested}^{-1}$) corresponds to the fraction of ingested carbon consumed by metabolic costs associated with feeding and assimilation, AE is the assimilation efficiency, and P_{egg} is the proportion of the assimilated food that is used for egg production.

Model 1: The first model was based in the original parameterization of K_m and I_{max} (Table I) by Møller *et al.* (2012), where P_{egg} was set to 1, i.e. this implies that the female biomass is kept constant, at the average measured carbon weight from 2008 (137 μgC female^{-1}).

Model 2: this is a fine tuning of the grazing parameters in Model 1. The half-saturation constant depends on food type and size composition and it is often necessary to recalibrate K_m to the given conditions (Møller *et al.*, 2012). Therefore, the K_m was recalibrated in order to try to obtain a better match with the timing of egg production.

Models 3 and 4: Egg production rates have been shown to increase during the spring bloom with a delay relative to grazing measured as fecal pellet production (Swalethorp *et al.*, 2011). At the same time, an increase in female carbon weight takes place (Swalethorp *et al.*,

Table I: Parameter values for the model to predict egg production

Parameter				Reference
Maximum ingestion	(μgC prey) (μgC copepod)$^{-1}$ d^{-1}	I_{max}	0.41	Møller *et al.* (2012)
Half saturation	μg Chl a L^{-1}	K_m	1	Møller *et al.* (2012)
Temperature threshold	Kelvin	P_1	293	Møller *et al.* (2012)
Temperature threshold	Kelvin	P_2	284	Møller *et al.* (2012)
Temperature threshold	Kelvin	P_3	13 282	Møller *et al.* (2012)
Temperature threshold	Kelvin	P_4	29 725	Møller *et al.* (2012)
Normalize factor		P_5	6.06[a]	Møller *et al.* (2012)
Assimilation efficiency	μgC (μgC ingested)$^{-1}$	AE	0.65	Møller *et al.* (2012)
Active metabolism	μgC (μgC ingested)$^{-1}$	R_a	0.25	Møller *et al.* (2012)
Basal metabolism	μgC (μgC biomass)$^{-1}$ d^{-1}	R_b	0.004	Møller *et al.* (2012), Maps *et al.* (2014)
Biomass by Jan. 1	μgC copepod^{-1}	B_{ini}	142	This study
Initial biomass	μgC copepod^{-1}	B_{min}	87	This study
Maximum biomass	μgC copepod^{-1}	B_{max}	202	This study

[a]Møller *et al.* (2012) erratum from earlier value of 5.72.

Table II: Model descriptions and performance of model predictions for specific egg production rate using correlation analysis and the Nash Sutcliffe Model efficiency (ME)

Model	Description	K_m	I_{max}	P_{egg}	Chl a	R^2	ME	Performance
1	Original	1	0.41	1	Total	0.47	−0.26	Poor
2	K_m modified	3.05	0.41	1	Total	0.43	0.24	Good
3	P_{egg} modified Chl a > 10 μm	1	0.41	variable	>10 μm	0.55	0.47	Good
4	P_{egg} modified Total Chl a	1	0.41	variable	Total	0.61	0.59	Very good

2011). We therefore include a dependency on female weight in the modelling of the weight-specific egg production by modifying P_{egg}.

P_{egg} varies with the biomass of the females (B, μgC). Egg production is initiated when the individual female biomass reaches a certain threshold (B_{min}, μgC) and increases until an upper threshold is reached and all carbon is allocated to eggs (B_{max}, μgC).

$$
\begin{aligned}
P_{egg} &= 0, \text{ for } B < B_{min}, \\
P_{egg} &= \frac{(B - B_{min})}{(B_{max} - B_{min})}, \text{ for } B_{ini} \leq B \leq B_{max}, \\
P_{egg} &= 1, \text{ for } B > B_{max}
\end{aligned}
\tag{5}
$$

The assimilated carbon not used for egg production is allocated for somatic growth, and the resulting change in body mass depends on grazing, egg production and respiration:

$$
\frac{dB}{dt} = B \cdot \left(g_i \cdot AE \cdot (1 - R_a) - R_b - SEP \right)
\tag{6}
$$

where R_b ($\mu gC_{resp} \ \mu gC_{copepod}^{-1} \ d^{-1}$) is the basal respiration (defined here as metabolic costs of non-dormant copepods in the absence of food), which at 0°C is assumed to be $0.007 \ \mu gC_{resp} \ \mu gC_{copepod}^{-1} \ d^{-1}$ (Maps *et al.*, 2014).

B_{min}, B_{max} and the biomass at the beginning of the year (B_{ini}, μgC) was estimated by fitting the model to the measurements of female biomass from 2008 (Swalethorp *et al.*, 2011) by applying a Generalized Reduced Gradient Algorithm (Excel) for optimizing nonlinear problems (Fig. 1). Model 3 considered only large phytoplankton, i.e. Chl *a* concentrations >10 μm, whereas Model 4 considered total Chl *a* concentrations.
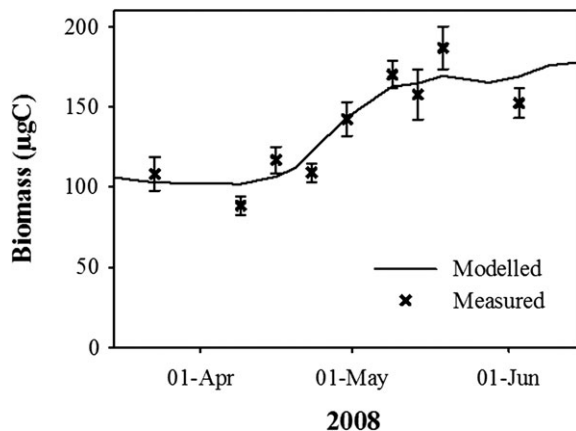
Fig. 1. Individual biomass of female *Calanus finmarchicus* (μgC) measured in 2008 in Disko Bay ± SE (Swalethorp *et al.*, 2011) and modelled biomass (Model 4).

The performance of the four suggested models was tested against all available data using Pearson correlation analysis (R^2, $\alpha = 0.05$) as a measure of the model capability to catch the seasonal variability. In addition, the Nash Sutcliffe Model Efficiency (ME) was used to estimate the predictive power of the model (Nash and Sutcliffe, 1970), which is a measure of the ratio of the model error to the variability of the data and hence:

$$
ME = 1 - \frac{\sum_{n=1}^{\mathcal{N}} (D - M)^2}{\sum_{n=1}^{\mathcal{N}} (D - \bar{D})^2}
\tag{7}
$$

where D is the observational data, M is the model data and the overbar indicates the average of the observed data, $\mathcal{N}$ is the total number of data pairs and n is the nth comparison. Performance levels are assessed as follows: >0.65 excellent, 0.50–0.65 very good, 0.20–0.50 good, and <0.20 poor (Allen *et al.*, 2007).

## RESULTS

In situ measurements in Disko Bay

In 2008, Disko Bay was ice covered for 4.5 months until the end of April. After the sea ice break up, the spring bloom developed quickly (Fig. 2) and an increase from 1 to 15 μg Chl *a* L^{-1} was observed in just 5 days. The Chl *a* concentration then remained at this level for about 2 weeks followed by a sharp decrease (Fig. 2). Maximum egg production rates (10–16 eggs female^{-1} d^{-1}, up to 0.03 μgC$_{egg}$ μgC$_{female}^{-1}$ d^{-1}) were observed about one week after the bloom peaked.

In 2011, the sea ice cover was unstable and the bloom started earlier (Fig. 2). The maximum Chl *a* level (11 μg Chl *a* L^{-1}) was lower than in 2008, but stayed high for about a month (Fig. 2).

In 2012, the ice cover was coherent until mid-April; later until mid-May a lot of drift ice was present. The phytoplankton bloom started when the ice broke and lasted until mid-May (Fig. 2).

Egg production rates were more variable in 2011 and 2012 than in 2008, but they remained high for a longer period (Fig. 2). The maximum egg production rate was 27 and 36 eggs female^{-1} d^{-1} (up to 0.06 μgC$_{egg}$ μgC$_{female}^{-1}$ d^{-1}) in 2011 and 2012, respectively. During the main bloom (end of April to mid-May) the cumulated egg production in 2011 and 2012 was more than twice as high as in 2008 (Fig. 3).

In all years, the *in situ* temperature in the upper 50 m of the water column was below 0°C during the bloom and until the end of May, when the surface layer was warming (Fig. 2).
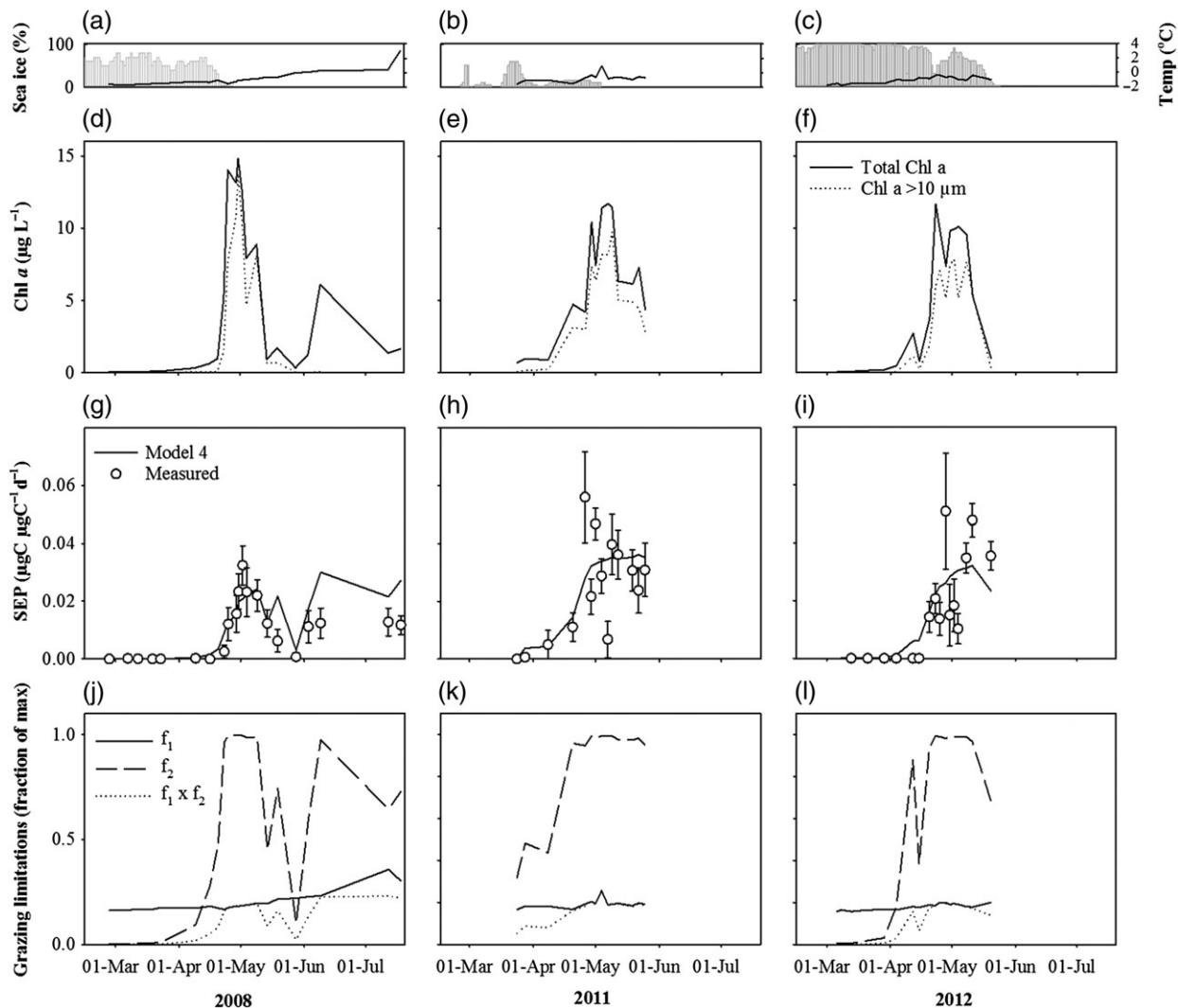
Fig. 2. (**a**)–(**c**) Ice cover (%), temperature at 20 m, (**d**)–(**f**) integrated (0–50 m) concentration of total and >10 μm Chl *a* (μg L⁻¹), (**h**)–(**j**) *Calanus finmarchicus* measured (±SE) and modelled specific egg production rate (SEP, μg C μg $C_{copepod}^{-1}$ d⁻¹) and (**k**)–(**m**) the potential limitation of temperature (f_1) and total Chl *a* (f_2) on grazing (Equations 1–4).

Model predictions of female biomass and egg production

Model 4, which considered increase in female biomass and total Chl *a* concentrations, showed the best fit to the data (Table II, Fig. 3). The model performance was 'very good' (ME = 0.59) according to the ME criteria and reproduced ($R^2 = 0.61$) the overall seasonal pattern although the measured egg production rates were quite variable (Fig. 2). The timing of the initiation of the egg production was particularly well reproduced by the model. Total Chl *a* was a better predictor of egg production than the Chl *a* fraction larger than 10 μm used in Model 3 with 'good' performance ($R^2 = 0.55$, ME = 0.47).

When all ingested carbon was allocated directly to egg production using the original grazing equation

($P_{egg} = 1$, Model 1), the modelled cumulated egg production rate doubled, and the modelled initiation of the egg production occurred about 2 weeks earlier (Fig. 3). This did not agree with the observations and the model performance was found to be 'poor' (ME = −0.26, $R^2 = 0.47$).

Model 2 with constant female biomass ($P_{egg} = 1$) was recalibrated to the egg production data by changing K_m (3.05 μg Chl *a* L⁻¹). Thereby the modelled onset of egg production and cumulated egg production improved in comparison to Model 1 and the model performance was considered as 'good' according to the ME criteria (ME = 0.24) and with $R^2 = 0.43$ (Table II and Fig. 3). However, the gradual response in egg production seen in the measurements and Model 1 to the changing Chl *a* concentration was not reproduced (Fig. 3).
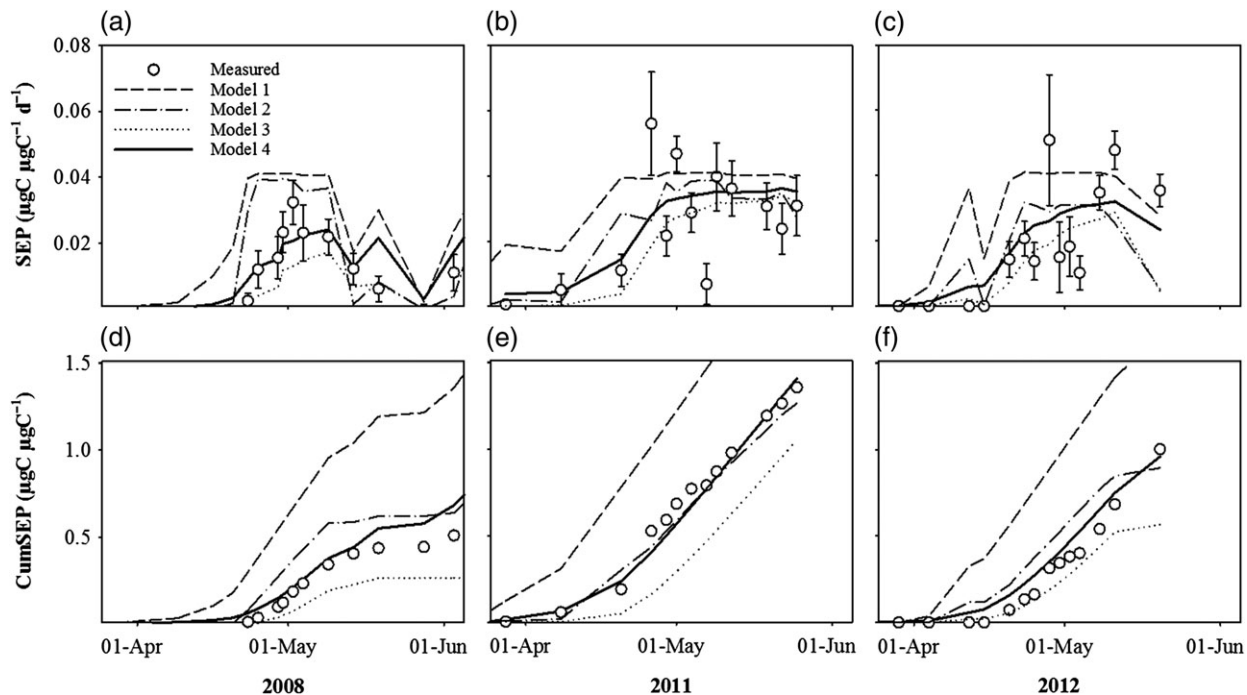
Fig. 3. Comparison of the measurements of *Calanus finmarchicus* egg production rate and the four different models setup tested (Table II) **(a)–(c)** is carbon specific egg production rate (SEP, µg C µg C$_{copepod}^{-1}$ d^{-1}) and **(d)–(f)** is the cumulated specific egg production (cumSEP, µg C µg C$_{copepod}^{-1}$) during the spring in Disko Bay 2008, 2011 and 2012.

Model predictions of limiting factors for grazing rates during the spring bloom

In all models, egg production rate ultimately depends on grazing of phytoplankton biomass, i.e. in models 1, 2 and 4 on total Chl *a* and in model 3 on Chl *a* >10 µm. Model 4 suggests that before initiation of the phytoplankton bloom, grazing will be more limited by food concentration ($f1 = 0$) than by temperature (Fig. 2). During the peak of the bloom with Chl *a* concentrations above ~4 µg Chl *a* L^{-1} ($f_1 > 0.95$), the grazing is in contrast food saturated, and increasing food concentration will not result in an increase in the grazing rate of more than a few percent. On the other hand, an increase in temperature of, e.g. 1°C during this period will lead to an increase in grazing rate of ~20% (Equations 1–3, Fig. 2). The period with food saturation was 16, 35 and 21 days in 2008, 2011 and 2012, respectively. The duration may even be longer in 2011 and 2012, because we stopped sampling before the bloom had quite ended.

DISCUSSION

Seasonal conditions and C. finmarchicus success

During the spring bloom, *C. finmarchicus* was food saturated. A short and intense phytoplankton bloom as in 2008 fuelled a lower cumulated egg production than longer lasting blooms as in 2011 and 2012. Thus, even though total new phytoplankton production was similar during the 3 years (Nielsen *et al.*, personal comment), the different bloom durations caused distinctively differences in the period where *C. finmarchicus* could maintain maximum egg production rate. Whether these higher egg production rates will transform into higher secondary production will obviously depend on factors influencing the standing stock such as mortality and advection. For example, the average *Calanus* spp. biomass during the spring was 10 times higher in 2008 than in 2005 (Madsen *et al.*, 2008; Swalethorp *et al.*, 2011). In the future, we assume that the production pattern will resemble 2011 and 2012 with less ice and/or recurrent wind mixing of the upper layer and a prolongation of the bloom. If in addition, temperature increases, this will amplify the positive effects on the cumulated egg production.

The temperature function in the models predicts that *C. finmarchicus* can produce eggs at about 15–20% of their maximum rate at −1.7 to 0°C (Equation 3). The predicted rates agree with those measured (Fig. 2), and the temperature response observed in laboratory (Hirche *et al.*, 1997; Kjellerup *et al.*, 2012). Hence, even in high Arctic areas reproduction should be able to sustain the population. However, a northward expansion will also depend on the ability of *C. finmarchicus* to complete development from egg to the overwintering

copepodite stage CV and to build up the lipid reserves needed for overwintering (Ji *et al.*, 2012).

In the Greenland Sea, *C. finmarchicus* females were able to reproduce at subzero temperatures, but only if sufficient food was present. Younger developmental stages were only present in areas where they or overwintering stages could have been advected from Atlantic waters suggesting that an overwintering population was not present (Hirche and Kosobokova, 2007). It has been suggested that even if *C. finmarchicus* produce eggs at subzero temperatures, nauplii may not be able to develop (Hirche and Kosobokova, 2007). Recent experiments have, however, shown that at least at 0°C the development rates of the nauplii stages were not different from what could be extrapolated from experiments carried out at higher temperatures (Grenvald *et al.*, 2012; Jung-Madsen and Nielsen, 2015). In Disko Bay, the first copepodite stages appear in May when temperatures are still below 0 (Madsen *et al.*, 2001; Swalethorp *et al.*, 2011). During summer the population takes advantage of the up to 7–8°C in the surface layers (Madsen *et al.*, 2001) and a local *C. finmarchicus* population can be sustained (Madsen *et al.*, 2001). Such relatively high surface summer temperatures are often found in stratified arctic waters (Sejr *et al.*, 2011; Flint *et al.*, 2015).

Model performance

Model 4 presented here allows prediction of egg production rates of *C. finmarchicus* from temperature and food concentration (total Chl *a*) during the spring bloom in Disko Bay. This appeared possible despite the different meteorological and ice conditions in the 3 years of the study, and though the parametrization of the model was implemented for the North Sea (i.e. at the southern border of the *C. finmarchicus* distribution; Møller *et al.*, 2012; Maar *et al.*, 2013). This may suggests a broad usage of the model across the habitats occupied by *C. finmarchicus* using this relatively simple parametrization. Some points to consider are described below.

One critical point is that initiation of egg production seems to be delayed if females are not fat enough when the spring bloom starts, i.e. that they need to feed to finalize gonad development. The weight of the females is known to vary across the spatial scale (Head *et al.*, 2013b), e.g. due to temperature or food conditions (Campbell *et al.*, 2001; Forster *et al.*, 2011). Thus, a standard weight cannot necessarily be applied everywhere, and knowledge of the local conditions are necessary.

In the present study, carbon measurements from 2008 clearly showed an increase in individual female biomass before egg production started (Fig. 1). Hence, the model needed to include allocation of the ingested carbon to biomass to describe the observed increase in

female biomass, but also to describe the timing of egg production. If all ingested carbon was assumed to go directly to egg production (Model 1), the modelled egg production would have started about 2 weeks earlier compared to the observations. Furthermore, the modelled cumulated egg production during the main bloom (until mid-May) would more than double which is clearly not in agreement with the measurements (Fig. 3). If we did not allow some of the ingested carbon to be allocated to female biomass increase, we needed to triple K_m to get the right timing in egg production in Model 2 (Fig. 3). Although this parametrization clearly does not acknowledge the female biomass changes, it is a way to achieve the right timing if unable to account for the female biomass in the model. A K_m of 3 is, however, high compared to *in situ* measurements across the North Atlantic of *C. finmarchicus* egg production dependency on Chl *a* (Melle *et al.*, 2014). On the Georges Bank, it was found to be ~0.5 µg Chl *a* L^{-1} (Runge *et al.*, 2006), while in the Labrador and Norwegian seas it was found to be 0.9 and 1.3 µg Chl *a* L^{-1}, respectively (Head *et al.*, 2013a). Few *in situ* studies have measured ingestion directly. Based on fecal pellet production rates, the half saturation for ingestion during the spring bloom in Disko Bay 2001 was 0.4 µg Chl *a* L^{-1} > 10 µm (Juul-Pedersen *et al.*, 2006). These measurements were based on short-term incubations (~2 h). In Disko Bay 2008, fecal pellet production was recorded in the egg production experiments (Swalethorp *et al.*, 2011). However, due to the long incubation time (~48 h) food may have been limiting, particularly at the lowest phytoplankton concentrations, and can therefore not be used to estimate the half saturation constant. For *Calanus glacialis/marshallae* in the Bering Sea a K_m of 2.5 was found for total Chl *a* at 0°C and ~1.5 for Chl *a* > 5 µm from bottle incubations (Campbell *et al.*, 2009). Modifying maximum ingestion rate, assimilation efficiency or active respiration rate will have the same proportional effect across temperature and food concentration (Table I).

Some studies have suggested that more southern populations of *C. finmarchicus* may, to some extent, produce eggs before they start feeding in the spring (Plourde and Runge, 1993; Richardson *et al.*, 1999). A potential explanation for that could be that if an individual has sufficient reserves left after hibernation, gonad maturation and egg production could start immediately. For example in the St. Lawrence Estuary, about 20 % of the *C. finmarchicus* population was able to produce eggs before the spring bloom without addition of food (Plourde and Runge, 1993). In the same study, a general decrease in the relative oil sac volumes before the spring bloom and throughout the productive season was observed. However, a delay in egg production after the phytoplankton bloom started accompanied by 50%

increase on the average oil sac volume was actually documented (Plourde and Runge, 1993), implying that although some individuals were able to produce eggs without food, the bulk of the population had to feed first. This agrees with the pattern documented in Disko Bay. During the main bloom, when gonads are fully matured, we expect the model to be able to predict egg production rates. Later in the season, the females may decrease egg production rate (Head *et al.*, 2013b), and predictions from the model may overestimate egg production. The model may be improved by taking into account female condition, i.e. the accumulated effect of previous feeding conditions.

In the present study, we used chlorophyll *a* as a proxy for the available food. This will conceal underlying preferences for different phytoplankton species and omit the protozooplankton fraction of the diet. However, during the bloom protozooplankton biomass co-varies with phytoplankton biomass, and as the copepods are food saturated it will not affect the egg production rate (Levinsen *et al.*, 2000; Madsen *et al.*, 2001). Outside spring bloom events, it is more important to include other prey types, e.g. protozooplankton (Levinsen *et al.*, 2000), and also consider that some part of the phytoplankton may not be available to copepods (Maar *et al.*, 2002). Particularly when copepods are not food saturated, it is important to consider food quality and availability since the modelled egg production rates in this situation will scale directly with the food concentration. Another potential food source not included in the model is ice algae. It is, however, unlikely that they are important in Disko Bay. During work on the ice, no ice algae were observed. Furthermore, content of the dietary lipid triacylglycerol in *C. finmarchicus* was low at the beginning of the bloom in 2008 suggesting that the copepods had not been feeding (Swalethorp *et al.* 2011).

Conclusion

To predict the success of *C. finmarchicus* in a changing climate, it is necessary to consider the combined effects of factors influencing reproduction, growth and survival. Our study on reproduction shows that at subzero temperatures *C. finmarchicus* can reproduce, but for the population to prevail, the length of the productive season has to allow development to the overwintering CV stage. Development time depends both on temperature and food concentration, and if temperature increases, development could be completed within a shorter productive season. Furthermore, higher temperatures would increase the egg production rate (Hirche *et al.*, 1997; Kjellerup *et al.*, 2012). Copepods were food saturated during the spring bloom in Disko Bay. This means that an increase in the magnitude of the spring bloom biomass will not affect egg production rates. On the other hand, changes in the duration of the spring bloom will translate into corresponding changes in the cumulated egg production rates, as seen from the differences between 2008 and 2011/2012.

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