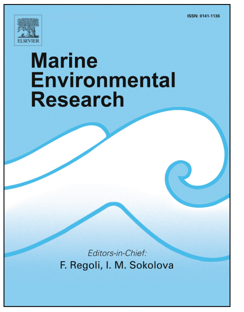
Accepted Manuscript



How including ecological realism impacts the assessment of the environmental effect of oil spills at the population level: The application of matrix models for Arctic *Calanus* species

Pepijn de Vries, Jacqueline Tamis, Morten Hjorth, Robbert Jak, Stig Falk-Petersen, Martine van den Heuvel-Greve, Chris Klok, Lia Hemerik

PII: S0141-1136(17)30674-8

DOI: 10.1016/j.marenvres.2018.09.008

Reference: MERE 4598

To appear in: *Marine Environmental Research*

Received Date: 3 November 2017

Revised Date: 4 May 2018

Accepted Date: 6 September 2018

Please cite this article as: de Vries, P., Tamis, J., Hjorth, M., Jak, R., Falk-Petersen, S., Heuvel-Greve, M.v.d., Klok, C., Hemerik, L., How including ecological realism impacts the assessment of the environmental effect of oil spills at the population level: The application of matrix models for Arctic *Calanus* species, *Marine Environmental Research* (2018), doi: 10.1016/j.marenvres.2018.09.008.

How including ecological realism impacts the assessment of the environmental effect of oil spills at the population level: the application of matrix models for Arctic *Calanus* species

Pepijn de Vries[1], Jacqueline Tamis[1], Morten Hjorth[2], Robbert Jak[1], Stig Falk-Petersen[3], Martine van den Heuvel-Greve[1], Chris Klok[1], Lia Hemerik[4]

[1]: Wageningen University and Research, Wageningen Marine Research, P.O. Box 57, 1780AB Den Helder, The Netherlands

[2]: COWI, Parallelvej 2, 2800 Kongens Lyngby, Denmark

[3]: Akvaplan-niva, Fram Centre for Climate and the Environment, N-9296 Tromsø, Norway

[4]: Wageningen University and Research, Biometris, Department of Mathematical and Statistical Methods, P.O. Box 16, 6700AA Wageningen, The Netherlands

Corresponding author: Pepijn de Vries, Wageningen University and Research, Wageningen Marine Research, P.O. Box 57, 1780AB Den Helder, The Netherlands E-mail: Pepijn.deVries@wur.nl

Abstract

For oil spill responses, assessment of the potential environmental exposure and impacts of a spill is crucial. Due to a lack of chronic toxicity data, acute data is used together with precautionary assumptions. The effect on the Arctic keystone (copepod) species *Calanus hyperboreus* and *Calanus glacialis* populations is compared using two approaches: a precautionary approach where all exposed individuals die above a defined threshold concentration and a refined (full-dose-response) approach. For this purpose a matrix population model parameterised with data from the literature is used. Population effects of continuous exposures with varying durations were modelled on a range of concentrations. Just above the chronic No Observed Effect Concentration (which is field relevant) the estimated population recovery duration of the precautionary approach was more than 300 times that of the refined approach. With increasing exposure concentration and duration, the effect in the refined approach converges to the maximum effect assumed in the precautionary approach.

Key words: matrix model, arctic, *Calanus*, LC50, NOEC, population dynamics, oil spill

Introduction

For oil spill planning and response decision-making it is important to assess and compare potential impacts of oil exposure on organisms present in the different ecosystem compartments. This might include the comparison of potential effects to aquatic organisms and their recovery times with the potential impact and recovery of coastal organisms and habitats. The process of Net Environmental Benefit Analysis (NEBA, IPIECA, 2015) has been developed to aid the response community in developing the response strategy that minimises the overall impacts to both humans and the environment. Assessment of the potential impact to valued ecosystem components is a crucial step within the NEBA process. For aquatic communities, this includes among others, the assessment of population impacts; based on (modelled) exposure concentrations, and the assessment of the fraction of the population exposed and affected. Effect assessments are usually based on data from laboratory toxicity testing (Olsen et al. 2013), where often only data on acute toxicity for a selected number of species are available. Thus, extrapolation techniques have been developed to derive chronic toxicity levels from acute toxicity data (e.g. by the use of a pragmatic acute to chronic ratio of for instance 10, see for example Ahlers et al. (2006)). Acute data is often used together with precautionary assumptions to derive threshold values covering for both short and long term effects of oil exposure, and these threshold values are often used in NEBA assessments (e.g. Coelho et al., 2015). A more refined approach is to use dose-response relationships applying varying exposure durations. The purpose of this study is to compare these two approaches and their consequences for the calculated population impacts (recovery duration) of a marine key stone species like *Calanus* and to assess the implications to oil spill response decision-making.

In this study, the focus is on herbivorous copepods of the genus *Calanus*, which are keystone organisms in the Arctic marine environment. *Calanus* species account for over half of the mesozooplankton biomass in some Arctic regions (e.g. the Svalbard region according to Søreide et al. (2008)), and link primary production to higher trophic levels, through the transfer of high energy lipids (Falk-Petersen et al. 2007). Based on the key role of the *Calanus* species in the pelagic food chain the potential population response of these species to an acute oil spill should further be investigated. In the present study two Calanus species (*Calanus glacialis* and *Calanus hyperboreus*) are selected to reflect the diversity in life-cycle structure of *Calanus* species.

The analytical tractability and the well-known behaviour of matrix population models (Caswell 2001), makes these models a simple and effective mean to translate individual toxicity data, e.g. No Observed Effect Concentrations (NOEC) and/or Median Lethal Effect Concentrations (LC50) to population level consequences (e.g. Caswell 1996; Klok and de Roos 1996; Hemerik and Klok 2006; Smit et al. 2006; Klok 2008; Klok et al. 2009; Bergek et al. 2012). The projection matrices are parameterised with the vital rates or life-history parameters, survival and reproduction.

An elasticity analysis was performed on age-structured matrix models to answer the question: how large is the effect of the relative change in length of diapause, survival and reproduction on the population growth factor? The matrix models were used for assessing population effects using two approaches for addressing effects of oil: 1) a precautionary approach where all exposed individuals survive below a chronic threshold concentration and die above this value or 2) a refined approach, in which a theoretical dose-response relationship was based on an acute to chronic ratio (ACR) that expresses the effect per toxic unit (TU). We want to assess the consequences for oil spill planning and response decision-making. Therefore, our main question is how these different approaches to effect assessment can lead to adjusted survival and reproduction parameters of individuals. These parameters are subsequently used to investigate and compare the effect of these two approaches on the population recovery of *Calanus* species.

Material and methods

Species selection

The arctic marine ecosystem consists for a large part of pelagic copepods and is dominated by three herbivorous *Calanus* species; *C. hyperboreus* (size 4.5-7 mm.), *C. glacialis* (3-4.6 mm.) and *C. finmarchicus* (size 2-3.2 mm.). These are key species in the lipid driven pelagic food chain and, consequently, they are important prey for zooplankton eating fish species, sea birds and mammals (Falk-Petersen et al. 2007). Therefore, a reduction in the copepod population, or a displacement of the various copepod species, potentially has extensive consequences for a wide variety of species in the Arctic food web. *C. hyperboreus* is a high Arctic oceanic species connected to the cold and ice covered deep Arctic Basin (Baffin Bay and the Greenland Sea), while *C. glacialis* has a slightly more southern circumpolar distribution along the Arctic shelf seas (Falk-Petersen et al. 2009, Daase et al. 2013). The two larger *Calanus* species form the major part of the biomass and *C. finmarchicus* is less adapted to life in the Arctic ocean (Hirche and Kosobokova 2007). De Hoop et al. (2016) has done a similar analysis for *C. finmarchicus* whereas our modelling work has focused on *C. glacialis* and *C. hyperboreus*.

Life-cycle of Calanus species

The life cycle of *Calanus* species consists of three main stages (fig 1a), namely eggs, nauplii larvae (N1-N6) and copepodites (C1-C5, and adult phase). *C. glacialis* has a 1-3 years' generation time with 2 years in most regions (Daase et al. 2013), whereas the generation time of *C. hyperboreus* varies between 1 and 6 years, depending on the geographical region and the food availability (Falk-Petersen et al. 2009).

Calanus species show seasonal vertical migration (Madsen et al. 2001; Falk-Petersen et al. 2009; Swalethorp et al. 2011). In winter, from January to March, eggs of *C. hyperboreus* are spawned deep in the water column being fuelled entirely by pre-existing, internal lipid reserves (Hirche 1997) and they float towards the surface. *C. glacialis* however, overwinters at shallower depths than *C. hyperboreus* and moves into the surface layer when ice algae bloom (Darnis and Fortier 2014). CG spawns near the surface around the time of the spring bloom (Madsen et al. 2001) and may rely on ice algae to fuel reproduction at the beginning of their growth season (Ji et al. 2012). A study performed in Disko Bay, Greenland, showed that *C. glacialis* ascended to the surface layer at the onset of the spring phytoplankton bloom, while two weeks later *C. hyperboreus* surfaced (Swalethorp et al. 2011). The timing of plankton blooms in the Arctic Ocean depends on the sea ice cover and thus differs per region. Generally, ice algae bloom one to two months before the ice melts and the phytoplankton bloom starts when the sea ice has disappeared, which is between May (at 75 ˚N) and August (at 85 ˚N) (Leu et al. 2011). A few months after the phytoplankton bloom, all *Calanus* species descend to overwintering depth. During overwintering *Calanus* species go in diapause, i.e. enter dormancy which is a phase of arrested development.

Temperature has a significant effect on the development times of *Calanus* eggs and nauplii stages (Corkett 1972; Corkett et al. 1986; McLaren et al. 1988; Jung-Madsen et al. 2013). From the first feeding stage (the third nauplius stage), food also becomes important (e.g. Jung-Madsen et al. (2013)). Effects of temperature and food availability on the impacts of oil exposure were outside the scope of this study and are therefore not included in this study. Furthermore, these conditions show great (spatial and temporal) variation in the field, making it difficult to define representative conditions. Here, we assume a region with optimal conditions enabling both *Calanus* species to complete their life cycle in two years and a more northern region, where the life cycle of *C. hyperboreus* is extended due to less favourable conditions (Falk-Petersen et al. 2009).

Model approach

A matrix population model was selected, because these models are often used given (1) their direct relationship with empirical, in our case, age-structured field data, (2) their clear link between life-history parameters (reproduction and survival) and population growth factor and (3) their relatively low data requirements (Beissinger and Westphal 1998). This is because we lump stages according to years and then we only require a few parameter values as can be seen in appendix A and ESM1. The life cycles of the copepods were simplified to always allow for a separate (reproducing) adult stage. The total number of juvenile and sub-adult stages were changed in models to allow for situations where reproduction starts after more than one year. The environment of the populations is assumed to be homogeneous, and the model is not spatially explicit.

For density independent matrix models elasticity analysis (this is a form of sensitivity analysis) can easily be performed. This analytical tool assesses the relative contribution to the population growth factor (λ) of the different underlying parameters. Elasticities represent the proportional change in λ given an infinitesimal proportional change in a matrix element or underlying parameter (Caswell 2001; de Kroon et al. 1986). When the parameter with the largest elasticity is changed, the proportional change in λ is at its highest.

The two matrix models assume a 2-year life cycle for *C. glacialis* and for *C. hyperboreus* occurring in the sub-Arctic (2x2 matrix model, see fig. A.1) and a 4-year life cycle for *C. hyperboreus* with a more polar distribution (4x4 matrix model; see fig 1b). Thus, we assumed that the generation time of *Calanus* species is two or four years depending on the geographical location of its development. Only females were modelled and a constant sex ratio of 1:1 is assumed. In the main text details and mathematical analysis for the 2x2-model and toxicity results for both models are supplied. The derivation and analysis of the 4x4-model can be found in the Electronic supplementary information (ESM1 section 1).

All presented population models start just after spawning. Due to a lack of reliable data, survival throughout the year was assumed to be based upon a constant daily survival probability. Also, the reproduction is evenly divided over the length of the reproductive season. As the consequences of the timing of a hypothetical oil spill within a year and population impact thereof are not part of the study aim, these assumptions have no influence on the results. Thus, outside the spawning season the daily reproductive rate is zero. For the life cycles with a generation time of two years the graphs and the details for deriving the matrix model on a year-to-year basis from the daily events are presented in Appendix A. The simulations are performed with the daily events, while the elasticity analysis is performed on the yearly matrices.

The 2x2-model is represented in figure A.1cd and based on the real life cycle (given in fig. A.1ab, in Appendix A). Thus, for the model with a generation time of two years the two classes $(x_0(t), x_1(t))^T$ represent the just born *Calanus* (0+ to one year old from here on referred to as juvenile), and 1+ (so older than one year from here on referred to as (sub)adults). The Leslie matrix for this system (Figure 1b) only has positive values on the places marked with a * (see equation 1; note that the time τ is measured in years). How these positive values are derived from daily based rates and what they look like in terms of daily survival and reproduction is explained in Appendix A.

$$\begin{pmatrix} x_0(\tau+1) \\ x_1(\tau+1) \end{pmatrix} = \begin{pmatrix} 0 & * \\ * & * \end{pmatrix} \begin{pmatrix} x_0(\tau) \\ x_1(\tau) \end{pmatrix} \qquad \text{eqn 1}$$

Based on data from the life cycle of *C. hyperboreus* it was considered that these crustaceans have a diapause period during the year, namely when they have migrated into the deep. In this period, it is assumed that no mortality and reproduction takes place (Figure 2), although in real life mortality during diapause can be substantial (Arnkværn et al. 2005; Daase et al. 2014).

Data for parameterisation of the matrix model

Literature has been searched for parameter values for our models. The detailed results can be found in ESM1 section 2. For the matrix model, 47 eggs laid per day per female was used for the reproduction during the bloom, i.e. the midpoint of the estimated range and assumes that this rate continues during one month (i.e. 30 days) resulting in 1410 eggs per *C. glacialis* female in one season. This corresponds well with reproduction rates observed in the laboratory. We assume the sex ratio to be 1:1, based on the genetically determined ratio, disregarding the ability of environmental factors to affect this ratio (Irigoien et al. 2000). We assume the length of the growth season for both *C. hyperboreus* and *C. glacialis* in the 2-year life cycle model to be 180 days (approx. 6 months per year). For the 4x4-model we assume it to be 120 days (approx. 4 months per year, electronic supplementary material (ESM1, section 1 fig S2, and section 2)). For parameterisation of the model daily survival probabilities (=1−daily mortality probabilities) are needed. We first assumed daily mortality probabilities close to the lowest value reported in literature 0.005 d^{-1}. However, with these values the population was not viable (yearly population growth factor <1). Because reproduction data from the literature were not so variable and the mortality rates were reported to be too high (Ankvaern et al. 2005; Thor et al. 2008; Daase et al. 2011; Jung-Madsen et al. 2013) we adjusted the survival probabilities based on the fixed reproduction rates and the length of the active growing season. This resulted in daily mortality probabilities below the range reported in the literature (see daily survival probabilities in Table 1). With the current choices for the parameter values the population is almost stable, i.e. showing a slight growth.

Toxicity

Information on the impact of oil-components on survival and reproduction in different developmental stages are relatively scarce (Olsen et al. 2013). Some effect values are available from recent studies (see ESM1, section 4 Table S.1) on *C. glacialis* exposed to oil mixtures (Hansen et al. 2011; Gardiner et al. 2013; Camus et al. 2015). However, crude oil is a complex mixture of both hydrocarbons, such as alkanes, cycloalkanes and aromatic hydrocarbons, and non-hydrocarbon compounds. Because crude oil has a variable composition, its effects on exposed biota also varies. Toxicological risks of oil mixtures are mostly determined by their dissolved components (e.g. French McCay 2002; Olsen et al. 2013). Therefore, in the current study, the exposure was expressed in Toxic Units (TU) (von der Ohe and de Zwart 2013) and these TUs are used to express the exposure to single oil components and to mixtures of oil components. To derive exposure values *x* (in TUs) from a (measured) compound concentration (*c*) we scale it with the acute LC50 concentration at which 50% of the organisms die:

$$x = \frac{c}{\mathrm{LC50}}. \qquad \text{eqn 2}$$

Here, we use a theoretical relation based on the ACR for Daphnia (May et al. 2016) to parameterise the concentration-time-response-relationship (approach 2) on the population growth factor. The definition of the ACR is the acute 50% effect concentration (LC50) divided by the chronic No Observed Effect Concentration (NOEC) for mortality:

$$\mathrm{ACR} = \frac{\mathrm{LC50}}{\mathrm{NOEC}} \qquad \text{eqn 3}$$

The scaled NOEC is called *n*: $n = \frac{\mathrm{NOEC}}{\mathrm{LC50}} = \frac{1}{\mathrm{ACR}}$. So if we know the NOEC concentration, and the ACR we can compute *x* in toxic units as $x = \frac{c}{\mathrm{ACR} \cdot \mathrm{NOEC}}$.

With this relationship we can compare our hypothetical relationship with real data.

Although oil toxicity can affect both reproduction and survival, we focus on toxic effects on survival. Because limited toxicity data are available for both *C. hyperboreus* and *C. glacialis,* a more theoretical approach was used to describe the relation between exposure and effect. For this approach, we assume that the hazard rate ($h(t)$, the probability per unit of time to die at time *t* conditional upon the subject still being alive (Kalbfleisch and Prentice, 2002) is a given function of exposure *x* (in TU) above the NOEC of *n* TU and the baseline or natural hazard rate $h_0(t)$:

$$h(t) = h_0(t)\exp(\beta \cdot \max(0, x - n)) \qquad \text{eqn 4}$$

The relationship is assumed to be multiplicative, and the magnitude of the effect is expressed as $\exp(\beta)$ per toxic unit above the NOEC. Because the exposure to oil is detrimental for the organisms $\exp(\beta) > 1$, and thus each extra toxic unit increases the natural hazard rate $h_0(t)$ with this factor. We assume that the natural daily hazard rate (d^{-1}) is constant in time (h_0) and is calculated as one minus the natural daily survival (used in the parameterisation of the matrix model, see above).

Because, in general, the hazard rate equals $h(t) = -\frac{\mathrm{d}\log(S(t))}{\mathrm{d}t}$ (Kalbfleisch and Prentice, 2002), the associated survivor function with this hazard rate is $S(t) = \exp(-\int_0^t h(\tau)\mathrm{d}\tau)$.

For a LC50 expressed as L TU determined at an acute exposure time of t_a days it holds that the surviving fraction of the exposed organisms at time t_a, $S(t_a)$, is half the surviving fraction of the unexposed organisms.

$$0.5 = \frac{\exp(-\int_0^{t_a} h_0(t)\exp(\beta \cdot \max(0, L-n))\mathrm{d}t)}{\exp(-\int_0^{t_a} h_0(t)\mathrm{d}t)} \qquad \text{eqn 5}$$

From this relationship we can for a constant baseline hazard (h_0), and an acute exposure duration of t_a days derive the formula for the effect (=exp(β)) as

$$\exp(\beta) = \left(1 + \frac{\ln(2)}{h_0 t_a}\right)^{\left(\frac{\mathrm{ACR}}{\mathrm{ACR\text{-}1}}\right)} \qquad \text{eqn 6}$$

An ACR value of 8.8 was used as derived for *Daphnia magna* by May et al. (2016) and an acute exposure time t_a of 2 days (as per OECD standards for *Daphnia* tests (OECD, 2004)).

The hazard rate approach is based on internal exposure concentrations, where the dose affects the natural mortality rate when it exceeds an internal concentration threshold (i.e., at the molecular receptor for the toxic effect). Oil spill scenarios are based on external concentrations (i.e., concentrations in the water compartment, surrounding the target species). Modelling toxico-kinetics (i.e., the balance between uptake and elimination of a toxicant in different species compartments) is outside the scope of this study. We, therefore, assume that there is an instantaneous equilibrium between internal and external concentrations. We also assume that this equilibrium can be described by a constant ratio, the bio-concentration factor, between the internal and external concentration. Because of these assumptions, the hazard model could be and was directly applied to external exposures when expressed as toxic units.

Similar to the LC50 the NOEC is based on specific external test concentrations, as selected by the experimenters. The No Effect Concentration (NEC) as applied in the hazards model is based on internal concentrations, and does not depend on selected test concentrations (Kooijman 2010). However, as test data availability is limited, we note that the ACR applies to internal and external concentrations that only differ by the bio-concentration factor (see the above assumption). Therefore, the NOEC was used as if it were a NEC. This also makes it possible to compare model simulations with experimental toxicology data that are available.

Approaches for assessing effects of exposure to toxic substances

In our simulations exposure to an oil spill was included during part of the year. Therefore, the *Calanus* population was modelled from day-to-day. In appendix A how to derive the year-to-year dynamics from the day-to-day dynamics for the population divided into two classes (2x2-model) and in ESM1 (section 1) for four classes (4x4-model) is presented.

The model simulates the Arctic *Calanus* species exposed to a range of TUs for a range of exposure durations (2, 4, 8 and 16 days) and a range of exposed fractions of the population. The exposure concentration is varied between 0.9/ACR (i.e., 90% of the NOEC) and 1.1 TU (i.e., 10% above the LC50) in 16 equidistant exponential steps and the exposed fraction of the population varies between 1 and 99% in nine equidistant linear steps.

The affected fraction indicates the fraction of the population that is being exposed to oil. So only that fraction will be affected, following one of two different approaches: 1) precautionary: all individuals exposed above the NOEC die instantaneously; 2) refined (full-dose-response): individuals die as the result of an increased hazard rate, which depends on the exposure concentration and duration (as described above). No exchange of individuals between the exposed and the unexposed fraction of the population is modelled. Recovery time is evaluated for the entire population (both exposed and unexposed).

The recovery time is expressed as the minimum time required to reach the same peak number of adult individuals (just after hatching) after an exposure. Because this definition is linked to the census moment, just after hatching, the recovery time is always expressed in number of full years starting at 1. In reality, recovery can occur during the year before the reported number of years.

For the precautionary approach this recovery time can be solved exactly (ESM1 section 3) and is expressed as follows:

$$T_r = \left[\left[\frac{-\log(1-f)}{\log(\lambda)}\right]\right] \qquad \text{eqn 4}$$

Where T_r is the recovery time in years, λ is the dominant eigenvalue of the population matrix (i.e., the population growth factor) and f is the exposed fraction of the population. The double square brackets indicate that the value is rounded to its ceiling integer value.

For the refined approach the assessment of the recovery time is more complicated and is obtained through simulation with the matrix model. The development of the *Calanus* population is simulated for a period of 102 years, where the exposure takes place in the third year, directly after hatching of the eggs. Only if full recovery takes less than 100 years, it can be calculated using this approach.

At each of the simulated exposed fraction, exposure concentration and exposure duration, the two approaches (precautionary and refined) are compared by the ratio R, which is obtained by dividing the recovery time for the precautionary approach 1 (T_{r1}) by the recovery time for the refined approach 2 (T_{r2}):

$$R = \frac{T_{r1}}{T_{r2}} \quad \text{eqn 5}$$

Results

Sensitivity and elasticity

When using the parameter values for the 2x2 and 4x4 models as depicted in Table 1 the yearly growth factor is respectively 1.02 and 1.01, meaning that both modelled populations are almost stable under normal conditions. The matrix model parameter with the highest elasticity is the adult survival (Table 2) in both models. Because all survival values have high elasticities, the modelled populations are limited by survival.

Model simulations

The maximum difference between the approaches depends on the fraction of the population that is exposed to the oil spill, but also on the yearly growth factor of the population (eqn 4, Figure 3). The yearly growth factor of the 4x4 population (λ=1.01) is slightly lower than that of the 2x2 model (λ=1.02). This difference in yearly growth factor results in a larger difference in recovery duration between the precautionary approach and the refined approach in the four life stages population than in the population with only two distinguished life stages.

Figure 3 shows how the recovery durations for the two approaches (precautionary and refined) expressed as ratio R, change as a function of exposure concentration (TU), exposure duration and the fraction of the population that is exposed.

In both approaches, there is no difference in effect below the NOEC, which is the result of our assumptions (i.e., no effects occur at or below the NOEC). Just above the NOEC the differences between the approaches are maximum (ratio of 211 and 329 when 99% of the population is exposed for the 2x2 and 4x4 model respectively): in the precautionary approach the fully exposed population dies instantaneously while the effect in the refined approach is relatively small (a daily increased mortality of 3% at a concentration 10% above the NOEC).

With increasing exposure concentration (0.1-1 TU), the effects in the refined approach differs less from the precautionary approach as can be seen in all panels of Figure 3. This is also the case with increasing exposure durations (2-16 days). This is because with increasing exposure concentration and duration, the effect in the refined approach approximates the maximum effect assumed in the precautionary approach.

When the exposed fraction of the population is higher (from 1% to 99% of the population exposed), the difference between the precautionary and the refined approach also becomes higher (from 0 to >300), as differences between the two are amplified when a larger portion (>1%) of the population is exposed.

Discussion

The matrix models

The population growth factor calculated with our matrix models, based on literature data on daily egg production and daily mortality rates, revealed that published mortality rates (see below) appear to be too high to maintain stable populations in unpolluted conditions. Based on this, the daily mortality probabilities in the simulations matrices were adjusted to reach stable populations under unpolluted conditions (no oil spill). With these values for the matrix model parameters a sensitivity and elasticity assessment showed that changes in daily mortality probabilities most heavily affect changes in population dynamics. This implies that realistic assessments of mortality rates over a relevant duration (e.g. life cycle of the species), and under relevant environmental conditions (those faced by the species) are very important to estimate the population level consequences of oil pollution. However, as described previously, estimation of realistic mortality rates in copepods is difficult, because rates are site and time dependent (Melle and Skjoldal 1998). The measurement of mortality rates in the laboratory or in the field often involves relatively short periods of time (order of days or weeks) when compared to the full life cycle of copepod species considered, ranging from two to more than four years. High mortality rates occur due to handling and catching individuals with nets, transfer to containers, transport to lab, and inspection under the microscope. Established field estimates of mortality shows high variability, and copepods often experience high mortality in the laboratory (Arnkværn et al. 2005; Thor et al. 2008; Daase et al. 2014; Skardhamar et al. 2011; Jung-Madsen et al. 2013; Weydmann et al. 2015). Reproduction estimates (both timing of reproduction and number of eggs produced) are also known to vary considerably (Melle & Skjoldal 1998; Madsen et al. 2001; Niehoff et al. 2002; Niehoff & Hirche 2005; Varpe et al. 2007; Swalethorp et al. 2011; Hirche 2013; Daase et al. 2013).

In constructing a matrix model another complication is that the development of copepods and therewith the generation time of *Calanus* spp. varies considerably, depending on geographical region and food availability (e.g. Falk-Petersen et al. 2009). Because of this high variability due to local conditions we did not strive for our model to represent a specific geographic location. Instead, fixed generation times were used under the assumption that they represent *C. glacialis* and *C. hyperboreus* that occur in the relatively mild polar range such as the Barents Sea (2x2 model). Furthermore, *C. hyperboreus* also occurs at more severe polar conditions such as the Kara Sea, Greenland Sea and Billefjorden (4x4 model), following the geographic regions as described by Falk-Petersen et al. (2009). The parameter values selected for the matrix models are also simplifications because mortality rates, growth and toxic effects on mortality rates, were assumed to be constant over life stages, whereas studies show that the various nauplii and copepodite stages may have different rates for growth and mortality (Arnkvaern et al. 2005, Grenvald et al. 2013).

By simplifying the real life cycle with all different stages (eggs, nauplii, copepodites, and adults) to a year-based model with average survival throughout the year, details were lost in the composition of the *Calanus* population with respect to the distribution over the different stages. However, this simple model for the dynamics of grouped juvenile and sub-adult classes is easily adapted to data on the effect of toxic substances. One of the main results of both matrix models is that the population growth factor is predominantly determined by the survival of the considered life stages. Within these yearly survival probabilities adult survival is relatively affecting the population growth factor the most. The combination of high uncertainty of and high sensitivity for these survival rates could have affected the estimated recovery durations results considerably.

In order to reflect a seasonal cycle, fixed periods of time were assumed in which reproduction, growth and diapause takes place. Neither growth nor mortality was assumed to take place during diapause, even though deaths are observed during this period (Daase et al. 2014). This also means that in our model oil spills have no impact during the diapause season. Because oil spills are often confined to the water surface layers and diapausing copepods migrate to deeper water layers, the probability that oil spills affect copepods during winter seems limited (Klok et al. 2012). Also, migration is not considered in the current matrix model as a mechanism for replenishing the population. This implies that there are restrictions to the spatial dimensions for the applicability of the model. The population considered is exposed to a defined concentration of toxic substance(s).

The toxicity model

The use of toxicity information into the model was limited for two reasons. Firstly, few studies have been published that assess the impact of oil or oil components on *C. glacialis* and *C. hyperboreus*. Secondly, when toxicity information is available the end-points used often do not fit into the life cycle parameters required for matrix models. Most of the available data consider acute or sub-chronic effects, i.e. the exposure duration is limited when compared to the full life cycle. There are no known studies that cover a significant part of the full life cycle of Arctic copepods. Although the toxicity of oil to *Calanus* species has been studied, indicating e.g. that sensitivity varies among *Calanus* species (Grenvald et al. 2013; Nørregaard et al. 2014), scarcity of the toxicity data limits the realistic prediction of population effects of specific exposures. Moreover, variance in acute mortality values can result in dramatically different population responses (Stark et al. 2015). The matrix model takes only the parameters of egg production, and mortality rates into account, and therefore several types of toxic impacts are not considered in the model. For instance, a reduction of growth may result in a delay of stage development. This could be fatal in case a particular stage is not reached in time to be able to go into diapause during winter (Klok et al. 2012).

The issues mentioned here are also a reason why precautionary measures are currently used, when assessing an oil spill impact.

In our study, we used TU to express exposure concentrations. The TU range applied in this study increases up to 1.1, which corresponds to an exposure concentration slightly above the LC50. Exposure above LC50 values can be realistic in field situations, especially directly after and/or near the source of a spill (Table 3). TUs in field situations based on concentrations from actual, experimental and modelled spills range between 0.00003 and 15.63, with most values below 0.1 TU. According to our modelling results this means that for field situations, the predicted impact based on the precautionary approach compared to the predicted impact based on the refined approach would in most cases lead to comparable results but could also be overestimated by a factor of 300 or more, especially when a larger part of the population is exposed.

In the present study, toxicants are assumed to instantaneously reach an equilibrium between external and internal concentrations. In the Arctic *Calanus* species studied here, this might not be realistic, given their high lipid content and relatively large size (particularly *C. hyperboreus*). Nordtug et al. (2015) compare relative oil clearance from *C finmarchicus* for different treatments but could not calculate absolute clearance rates due to technical limitations. De Hoop et al. (2013) indicate that excretion of oil constituents in aquatic is relatively slow. Consequently, effects calculated here may underrepresent the exposure duration and overestimate the exposure concentration for the refined approach.

Consequences for impact assessment

Whether a population recovers and within which time span critically depends on the migration between the exposed and unexposed fraction of the population. Therefore, the spatial scale of the spill should also be considered (as this also affects the fraction of the population being exposed). Recovery also depends on life history characteristics of the species that determine the population growth factor, which in turn determines the recovery rate, with a higher yearly population growth factor causing a faster recovery.

Based on our results the impact (i.e. population recovery duration) of an oil spill for the water column may be highly overestimated using the precautionary approach when exposure concentrations exceed threshold concentrations up to median effect concentrations, especially for relatively large spills (i.e. affecting a large fraction of the population). This may affect impact assessment and the selection of proper mitigation techniques in case of an oil spill. However, care should be taken to directly adopt this more refined approach into oil spill response strategies. Impact assessment used in evaluating options for oil spill response (i.e. NEBA) considers different compartments, e.g. the water column, the water surface and shore. If in all compartments a similar approach is used the relative effect between compartments can be compared correctly. Here, we only considered a more realistic approach in one of the compartments (water column). When a more realistic approach is also implemented in the other compartments (e.g. water surface and shore) the relative weight of the impacts makes sense. As long as this is not the case, care should be taken to compare the effects of more realistic approaches in some compartments and conservative approaches in other.

Better and more realistic estimates of the natural survival rate and the toxic effects on this rate are needed most to allow for a more realistic assessment of population level consequences of these *Calanus* species in the case of an oil spill. Additionally, better estimates of effects of oil compounds on reproduction of these *Calanus* species can further improve the prediction of our models.

The matrix model provides more realism to assessments traditionally based on simple risk characterisation ratios, where exposure concentrations are divided by predicted no effect concentration. The matrix model can translate estimated effects to the population level. The simplifications applied in the model and the lack of data to parameterise the model, however, make the interpretation of the model results indicative in the absolute assessment of oil spill impacts. By comparing the two approaches on a relative scale, an indication of the level of conservatism for the precautionary approach is obtained. It implies that the current NEBA which uses the precautionary approach does not underestimate the effect imposed on populations by oil spills.

Acknowledgments

Work presented in this publication is performed as contract research funded by The International Association of Oil & Gas Producers (IOGP), as part of the project entitled 'Environmental Effects of Arctic Oil Spills and Arctic Oil Spill Response Technologies'. We thank Elisabeth van Ast-Gray for improving the use of English in the manuscript.

References

Agersted MD, Moller EF, Gustavson K (2018) Bioaccumulation of oil compounds in the high-Arctic copepod *Calanus hyperboreus*. Aquat Tox 195: 8-14

Ahlers J, Riedhammer C, Vogliano M, Ebert R-U, Kühne R, Schüürmann G (2006) Acute to chronic ratios in aquatic toxicity—variation across trophic levels and relationship with chemical structure. Environ Toxicol 25(11): 2937-2945

Arnkværn G, Daase M, Eiane K (2005) Dynamics of coexisting *Calanus finmarchicus*, *Calanus glacialis* and *Calanus hyperboreus* populations in a high-Arctic fjord. Polar Biol 28: 528–538

Beissinger SR, Westphal MI (1998) On the use of demographic models of population viability in endangered species management. J Wildl Manage 62: 821–841

Bergek S, Ma Q, Vetemaa M, Franzen F, Appelberg M (2012) From individuals to populations: Impacts of environmental pollution on natural eelpout populations. Ecotoxicol Environ Saf 79: 1–12

Boehm PD. Neff JM, Page DS (2007) Assessment of polycyclic aromatic hydrocarbon exposure in the waters of Prince William Sound after the Exxon Valdez oil spill: 1989-2005. Mar Pollut Bull 54(3): 339-356. doi: 10.1016/j.marpolbul.2006.11.025

Camus L, Brooks S, Geraudie P, Hjorth M, Nahrgang J, Olsen GH, Smit MGD (2015) Comparison of produced water toxicity to Arctic and temperate species. Ecotoxicol EnvironSaf 113(0): 248-258

Caswell H (2001) Matrix Population Models, 2nd edition. Sinauer Assiociates, Inc, Massachusetts, Sunderland.

Caswell H (1996) Demography meets ecotoxicology: untangling the population level effects of toxic substances. In: Newman, M.C., Jagoe, C.H. (Eds.), Ecotoxicology: A hierarchial treatment. Lewis Publishers, Boca Raton, USA, pp. 255–292

Coelho G.M., D. V. Aurand, J. Staves, E. Miller, A. Slaughter (2015) Net Environmental Benefit Analysis in Support of the Shelburne Basin Venture Exploration Drilling Project. Nova Scotia, Canada. June 2015. Prepared by HDR Inc. Accessed on November 15, 2016 at: http://www.cnsopb.ns.ca/sites/default/files/pdfs/oa_19i-_neba_rev2_-_2015-06-26.pdf

Corkett CJ (1972) Development rate of copepod eggs of the genus *Calanus*. J Exp Mar Bio Ecol 10: 171-175

Corkett CJ, McLaren IA, Sevigny JM (1986) The rearing of the marine Calanoid copepods *Calanus finmarchicus* (Gunnerus), *C. glacialis* Jaschnov and *C. hyperboreus* Kroyer with comment on the equiproportional rule. Syllogeus 58: 539-546

Daase M, Søreide JE, Martynova D (2011) Effects of food quality on naupliar development in *Calanus glacialis* at subzero temperatures. Mar Ecol Prog Ser 429: 111–124

Daase M, Falk-Petersen S, Varpe Ø, Darnis G, Søreide JE, Wold A, Leu E, Berge J, Philippe B, Fortier L (2013) Timing of reproductive events in the marine copepod *Calanus glacialis*: a pan-Arctic perspective. Can J Fish Aquat Sci 70: 871-884

Daase M, Varpe O, Falk-Petersen S (2014) Non-consumptive mortality in copepods: Occurrence of *Calanus* spp. Carcasses in the Arctic Ocean during winter. J Plankton Res 36: 129–144

Darnis G, Fortier L (2014) Temperature, food and the seasonal vertical migration of key arctic copepods in the thermally stratified Amundsen Gulf (Beaufort Sea, Arctic Ocean) J Plankton Res 36: 1092–1108

Faksness L-G, Brandvik PJ, Daae RL, Leirvik F, Børseth JF (2011) Large-scale oil-in-ice experiment in the Barents Sea: monitoring of oil in water and MetOcean interactions. Mar Pollut Bull 62: 976–984

Falk-Petersen S, Timofeev S, Pavlov V, Sargent JR (2007) Climate variability and possible effects on arctic food chains: The role of Calanus. Pages 147-166 in: Ørbæk JB,Tombre T, Kallenborn R, Hegseth E, Falk-Petersen S, Hoel AH (Eds.), Arctic Alpine Ecosystems and People in a Changing Environment, Springer Verlag, Berlin. 433 p.

Falk-Petersen, S, Mayzaud P, Kattner G, Sargent JR (2009) Lipids and life strategy of Arctic *Calanus*. Mar Biol Res 5: 18–39

Falk-Petersen S (2010) Consequences of changing ice cover for primary and secondary producers in the Arctic. Arctic Frontiers Tromsø 2010, YSF workshop Skiboten, 2 February 2010.

French McCay DP (2002) Development and application of an oil toxicity and exposure model, OilToxEx. Environ Toxicol Chem 21(10): 2080-2094

Gardiner WW, Word JQ,.Word JD, Perkins RA, Mcfarlin KM, Hester BW, Word LS, Ray CM (2013) The acute toxicity of chemically and physically dispersed crude oil to key arctic species under arctic conditions during the open water season. Environ Toxicol Chem 32 (10): 2284-2300. doi: 10.1002/etc.2307

Grenvald JC, Nielsen TG, Hjorth M (2013) Effects of pyrene exposure and temperature on early development of two co-existing Arctic copepods. Ecotoxicology 22(1): 184-198

Hansen BH, Altin D, Rorvik SF, Overjordet IB, Olsen AJ, Nordtug T, (2011) Comparative study on acute effects of water accommodated fractions of an artificially weathered crude oil on *Calanus finmarchicus* and *Calanus glacialis* (Crustacea: Copepoda). Sci Total Environ 409: 704-709.

Hemerik L, Klok C (2006) Conserving declining species: what help can we expect from the use of matrix population models? Anim Biol 56: 519–533

Hirche HJ (1989) Egg production of the Arctic copepod *Calanus glacialis*: laboratory experiments. Mar Biol 103: 311 -318

Hirche HJ (1997) Life cycle of the copepod *Calanus hyperboreus* in the Greenland Sea. Mar Biol 128: 607–618

Hirche HJ (2013) Long-term experiments on lifespan, reproductive activity and timing of reproduction in the Arctic copepod *Calanus hyperboreus*. Mar Biol 160: 2469–2481

Hirche HJ, Kosobokova K (2007) Distribution of *Calanus finmarchicus* in the northern North Atlantic and Arctic Ocean—Expatriation and potential colonization, Deep Sea Res Part II: Top. Stud. Oceanogr 54: 2729-2747

Hoop L de, Broch OJ. Hendriks AJ, De Laender F (2016) Crude oil affecting the biomass of the marine copepod *Calanus finmarchicus*: Comparing a simple and complex population model. Mar Environ Res 119: 197-206

Hoop L de, Huijbregts MAJ, Schipper AM, Veltman K, De Laender F, Viaene KPJ, Klok C, Hendriks AJ (2013) Modelling bioaccumulation of oil constituents in aquatic species. Mar Pollut Bull 76: 178-186

IPIECA (2015) Response Strategy Development Using Net Environmental Benefit Analysis (NEBA), IOGP report 527. http://www.ipieca.org/resources/good-practice/response-strategy-development-using-net-environmental-benefit-analysis-neba-good-practice-guidelines-for-incident-management-and-emergency-response-personnel/

Irigoien X, Obermüller B, Head RN, Harris RP, Rey C, Hansen BW, Hygum BH, Heath MR, Durbin EG (2000) The effect of food on the determination of sex ratio in Calanus spp.: evidence from experimental studies and field data. ICES J Mar Sci, 57: 1752–1763.

Jensen LK, Carroll J (2010) Experimental studies of reproduction and feeding for two Arctic-dwelling Calanus species exposed to crude oil. Aquat Biol 10 (3): 261-271. doi: 10.3354/ab00286

Ji RB, Ashjian CJ, Campbell RG, Chen CS, Gao GP, Davis CS, Cowles GW, Beardsley RC (2012) Life history and biogeography of *Calanus* copepods in the Arctic Ocean: An individual-based modeling study. Prog Oceanogr 96: 40–56

Jung-Madsen S, Nielsen TG, Grønkjær P, Hansen BW, Møller EF (2013) Early development of *Calanus hyperboreus* nauplii: Response to a changing ocean. Limnol Oceanogr 58: 2109–2121

Jung-Madsen S and Nielsen TG (2015) Early development of *Calanus glacialis* and *C. finmarchicus*. Limnol Oceanogr 60 (3): 934-946

Kalbfleisch JD, Prentice RL (2002) The statistical analysis of failure time data. (2nd edition) John Wiley & Sons, Inc.

Klok C, Roodbergen M, Hemerik L (2009) Diagnosing demographic data of declining wader populations with a matrix model. Anim Biol 59: 207–218

Klok C (2008) Gaining insight in the interaction of zinc and population density with a combined Dynamic Energy Budget- and population model. Environ Sci Technol 42: 8803–8808

Klok C, de Roos AM (1996) Population level consequences of toxicological influences on individual growth and reproduction in *Lumbricus rubellus* (Lumbricidae, Oligochaeta). Ecotoxicol Environ Saf 33: 118–127

Klok C, Hjorth M, Dahllöf I (2012) Qualitative use of Dynamic Energy Budget theory in ecotoxicology. Case study on oil contamination and Arctic copepods. J Sea Res 73: 24-31

Kooijman, S.A.L.M. (2010) Dynamic Energy Budget Theory for Metabolic Organisation. third ed. Cambridge University Press, UK

Kroon H de, Plaisier A, Groenendael J van, Caswell H (1986) Elasticity: the relative contribution of demographic parameters to population growth rate. Ecology 67: 1427–1431

Leu, E, Søreide JE, Hessen DO, Falk-Petersen S, Berge J (2011) Consequences of changing sea-ice cover for primary and secondary producers in the European Arctic shelf seas: Timing, quantity, and quality, Progress in Oceanography 90 (1–4) pp. 18-32.

Madsen SD, Nielsen TG, Hansen BW (2001) Annual population development and production by *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus* in Disko Bay, western Greenland. Mar Biol, 139 (1): 75-93

May M, Drost W, Germer S, Juffernholz T, Hahn S (2016) Evaluation of acute-to-chronic ratios of fish and Daphnia to predict acceptable no-effect levels. Environ Sci Eur 28: 16. doi:10.1186/s12302-016-0084-7

McLaren I A, Sevigny J-M, Corkett C J (1988) Body sizes, development rates, and genome sizes among *Calanus* species. Hydrobiologia 167/168: 275-284

Melle W, Skjoldal HR (1998) Reproduction and development of *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus* in the Barents Sea. Mar Ecol Prog Ser 169: 211–228

Niehoff B, Hirche HJ (2005) Reproduction of *Calanus glacialis* in the Lurefjord (western Norway): indication for temperature-induced female dormancy. Mar Ecol Prog Ser 285: 107–115

Niehoff B, Madsen SD, Hansen BW, Nielsen TG (2002) Reproductive cycles of three dominant *Calanus* species in Disko Bay, West Greenland. Mar Biol 140: 567–576

Nordtug T, Olsen AJ, Salaberria I, Øverjordet IB, Altin D, Størdal IF, Hanseny BH (2015) Oil droplet ingestion and oil fouling in the copepod *Calanus finmarchicus* exposed to mechanically and chemically dispersed crude oil. Environ Toxicol Chem 34(8): 1899-1906

Nørregaard RD, Nielsen TG, Møller EF, Strand J, Espersen L, Møhl M. 2014. Evaluating pyrene toxicity on Arctic key copepod species *Calanus hyperboreus*. Ecotoxicology 23(2):163-174.

OECD (2004) Test No. 202: Daphnia sp. Acute Immobilisation Test. OECD Publishing, Paris. doi: http://dx.doi.org/10.1787/9789264069947-en

Olsen GH, Klok C, Hendriks AJ, Geraudie P, De Hoop L, De Laender F, Farmen E, Grøsvik BE, Hansen BH, Hjorth M, Jansen CR, Nordtug T, Ravagnan E, Viaene K, Carroll J (2013) Toxicity data for modeling impacts of oil components in an Arctic ecosystem. Mar Environ Res 90: 9–17

Schroeder Gearon M, French McCay D, Chaite E, Zamorski S, Reich D, Rowe J, Schmidt-Etkin D (2014) SIMAP Modelling of Hypothetical Oil Spills in the Beaufort Sea for World Wildlife Fund (WWF). April 17, RPS Group plc Applied Science Associates and Environmental Research Consulting. South Kingstown, USA. http://awsassets.wwf.ca/downloads/wwf_beaufort_sea_oil_spill_modelling_full_report_rps_asa.pdf

Skardhamar J, Reigstad M, Carroll J, Eiane K, Riser CW, Slagstad D (2011) Effects of mortality changes on biomass and production in *Calanus* spp. Populations. Aquat Biol 12 (2): 129-145

Smit MGD, Kater BJ, Jak RG, Heuvel-Greve MJ van den (2006) Translating bioassay results to field population responses using a Leslie-matrix model for the marine amphipod *Corophium volutator*. Ecol Modell 196: 515–526

Søreide JE, Falk-Petersen S, Nøst Hegseth E, Hop H, Carroll ML, Hobson KA, Blachowiak-Samolyk K (2008) Seasonal feeding strategies of *Calanus* in the high-Arctic Svalbard region, Deep Sea Research Part II: Topical Studies in Oceanography 55 (20–21): 2225-2244

Stark J.D., Vargas R.I., Banks J.E. (2015) Incorporating variability in point estimates in risk assessment: Bridging the gap between LC50 and population endpoints. Environ. Toxicol. Chem. 34 (7): 1683-1688. doi: 10.1002/etc.2978

Swalethorp R, Kjellerup S, Dünweber M, Nielsen TG, Møller EF, Rysgaard S, Hansen BW. (2011) Grazing, egg production, and biochemical evidence of differences in the life strategies of *Calanus finmarchicus, C. glacialis* and *C. hyperboreus* in Disko Bay, Western Greenland. Mar Ecol Prog Ser 429:125-144

Thor P, Nielsen TG, Tiselius P (2008) Mortality rates of epipelagic copepods in the post-spring bloom period in Disko Bay, western Greenland. Mar Ecol Prog Ser 359: 151–160

Varpe Ø, Jørgensen C, Tarling GA, Fiksen Ø. (2007) Early is better: Seasonal egg fitness and timing of reproduction in a zooplankton life-history model. Oikos 116(8):1331-1342

Von der Ohe P.C., de Zwart D. (2013) Toxic Units (TU) Indicators. pp 1161-1170. In: J.-F. Férard, C. Blaise (eds.), Encyclopedia of Aquatic Ecotoxicology, Springer Science+Business Media, Dordrecht, the Netherlands.

Weydmann A, Zwolicki A, Muś K, Kwaśniewski S (2015) The effect of temperature on egg development rate and hatching success in *Calanus glacialis* and *C. finmarchicus.* Polar Res 34. doi:10.3402/polar.v34.23947

Appendix A

Life cycle graphs

In the region of the Fram Strait (Greenland Sea) both our focal *Calanus* species have a generation time of two years (Falk-Petersen, 2010). Here, individuals advance during the first year to the life stage where diapause can be initiated: copepodite stage three (C3) for *C. hyperboreus* and copepodite stage four (C4) for *C. glacialis* (based on Falk-Petersen et al. 2009).

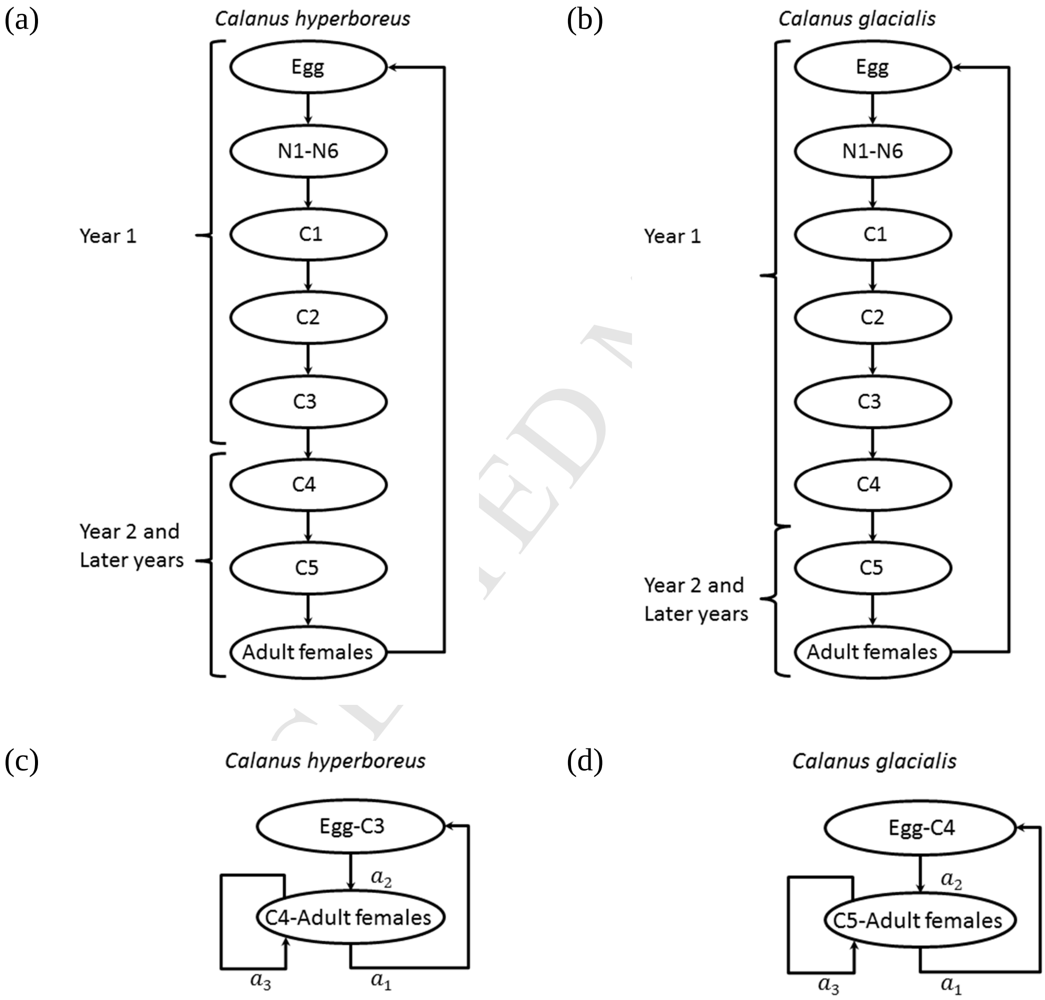


Figure A.1: the real (panels a and b) and modelled (panels c and d) life cycle with generation time of two years of *C. hyperboreus* and *C. glacialis.* N1-N6: nauplii stages 1-6; C1-C5: copepodite stages 1-5; a_1: reproductive value; a_2: survival to adult female and a_3: yearly survival of adult females.

From days to year

$$\begin{pmatrix} v_0(\tau+1) \\ v_1(\tau+1) \end{pmatrix} = \begin{pmatrix} 0 & a_1 \\ a_2 & a_3 \end{pmatrix} \begin{pmatrix} v_0(\tau) \\ v_1(\tau) \end{pmatrix} \qquad \text{eqn A.1}$$

$$\begin{pmatrix} v_0(t+1) \\ v_1(t+1) \end{pmatrix} = \begin{pmatrix} s_0 & 0 \\ 0 & s_1 \end{pmatrix} \begin{pmatrix} v_0(t) \\ v_1(t) \end{pmatrix} \quad \text{for } t = 1,\ldots,(365-w-b) \qquad \text{eqn A.2}$$

Accounting for diapause in which everyone survives gives eqn. A.3

$$\begin{pmatrix} v_0(t+1) \\ v_1(t+1) \end{pmatrix} = \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix} \begin{pmatrix} v_0(t) \\ v_1(t) \end{pmatrix} \quad \text{for } t = (366-w-b),\ldots,(365-b) \qquad \text{eqn A.3}$$

$$\begin{pmatrix} w(t+1 \\ v_0(t+1) \\ v_1(t+1) \end{pmatrix} = \begin{pmatrix} 0 & \frac{m}{2}s_1 \\ s_0 & 0 \\ 0 & s_1 \end{pmatrix} \begin{pmatrix} v_0(t) \\ v_1(t) \end{pmatrix} \quad \text{for } t = 366-b \qquad \text{eqn A.4}$$

Subsequently the spawning season lasts for $b-1$ days:

$$\begin{pmatrix} w(t+1 \\ v_0(t+1) \\ v_1(t+1) \end{pmatrix} = \begin{pmatrix} s_0 & 0 & \frac{m}{2}s_1 \\ 0 & s_0 & 0 \\ 0 & 0 & s_1 \end{pmatrix} \begin{pmatrix} w(t) \\ v_0(t) \\ v_1(t) \end{pmatrix} \quad \text{for } t = (367-b),\ldots,365 \qquad \text{eqn A.5}$$

Just after the spawning season we have to return to the original two classes:

$$\begin{pmatrix} v_0(t+365) \\ v_1(t+365) \end{pmatrix} = \begin{pmatrix} 1 & 0 & 0 \\ 0 & 1 & 1 \end{pmatrix} \begin{pmatrix} w(t+365^-) \\ v_0(t+365^-) \\ v_1(t+365^-) \end{pmatrix} \qquad \text{eqn A.6}$$

In total the year-to-year matrix, with time τ represented in years, is:

$$\begin{pmatrix} v_0(t+1) \\ v_1(t+1) \end{pmatrix} = \begin{pmatrix} 0 & \frac{m}{2} s_1^{366-b-w} \frac{s_0^{\,b} - s_1^{\,b}}{s_0 - s_1} \\ s_0^{\,365-w} & s_1^{\,365-w} \end{pmatrix} \begin{pmatrix} v_0(t) \\ v_1(t) \end{pmatrix} \qquad \text{eqn A.7}$$

The characteristic equation for this matrix is given in eqn A.8, and the dominant eigenvalue is

$$\lambda_d = 0.5 s_1^{\,365-w} + 0.5\sqrt{\left(s_1^{\,365-w}\right)^2 + 2m\left(s_0 s_1\right)^{365-w} s_1^{\,1-b}\left(\frac{s_0^{\,b} - s_1^{\,b}}{s_0 - s_1}\right)}.$$

$$\lambda^2 - s_1^{\,365-w}\lambda - \frac{m}{2}\left(s_0 s_1\right)^{365-w} s_1^{\,1-b}\left(\frac{s_0^{\,b} - s_1^{\,b}}{s_0 - s_1}\right) = 0 \qquad \text{eqn A.8}$$

It should be noted that in the elasticities below the logarithm log(x) is the natural logarithm.

$$e(b) = \frac{b}{\lambda}\frac{\partial\lambda}{\partial b} == \frac{\frac{bm}{2}\log\left(\frac{s_0}{s_1}\right)(s_0 s_1)^{365-w} s_1\left(\frac{s_0}{s_1}\right)^b}{\lambda\left(2\lambda - s_1^{\,365-w}\right)\left(s_0 - s_1\right)} \qquad \text{eqn. A.9}$$

$$e(s_0) = \frac{s_0}{\lambda}\frac{\partial\lambda}{\partial s_0} = \frac{\frac{m}{2} s_0 \left(s_0 s_1\right)^{365-w}\left(\left((365-w+b)\left(\frac{s_0}{s_1}\right)^{b-1} - (365-w)\left(\frac{s_0}{s_1}\right)^{-1}\right)\left(s_0 - s_1\right) - s_1\left(\left(\frac{s_0}{s_1}\right)^b - 1\right)\right)}{\lambda\left(2\lambda - s_1^{\,365-w}\right)\left(s_0 - s_1\right)^2} \qquad \text{eqn A.10}$$

$$e(s_1) = \frac{s_1}{\lambda}\frac{\partial\lambda}{\partial s_1} = \frac{(365-w)\, s_1^{\,365-w}}{\left(2\lambda - s_1^{\,365-w}\right)} + \frac{\frac{m}{2} s_1 \left(s_0 s_1\right)^{365-w}\left(\left((366-w-b)\left(\frac{s_0}{s_1}\right)^b + (366-w)\right)\left(s_0 - s_1\right) + s_1\left(\left(\frac{s_0}{s_1}\right)^b - 1\right)\right)}{\lambda\left(2\lambda - s_1^{\,365-w}\right)\left(s_0 - s_1\right)^2} \qquad \text{eqn A.11}$$

$$e(m) = \frac{m}{\lambda}\frac{\partial\lambda}{\partial m} = \frac{\frac{m}{2}\left(s_0 s_1\right)^{365-w} s_1\left(\left(\frac{s_0}{s_1}\right)^b - 1\right)}{\lambda\left(2\lambda - s_1^{\,365-w}\right)\left(s_0 - s_1\right)} \qquad \text{eqn A.12}$$

$$e(w) = \frac{w}{\lambda}\frac{\partial\lambda}{\partial w} = \frac{-w\log(s_1) s_1^{\,365-w}}{\left(2\lambda - s_1^{\,365-w}\right)} - \frac{\frac{m}{2} w\ln(s_0 s_1)(s_0 s_1)^{365-w} s_1\left(\left(\frac{s_0}{s_1}\right)^b - 1\right)}{\lambda\left(2\lambda - s_1^{\,365-w}\right)\left(s_0 - s_1\right)} \qquad \text{eqn A.13}$$

References for Appendix A

Falk-Petersen, S, Mayzaud P, Kattner G, Sargent JR (2009) Lipids and life strategy of Arctic *Calanus*. Mar Biol Res 5: 18–39

Falk-Petersen S (2010) Consequences of changing ice cover for primary and secondary producers in the Arctic. Arctic Frontiers Tromsø 2010, YSF workshop Skiboten, 2 February 2010

Tables

Table 1**:** The parameter values required for the matrix model year-to-year projecting and the simulation model for daily accounting the population development. For the 2 year life cycle the population growth factor with these parameter values is 1.02, while it is 1.01 for the 4 year life cycle.

parameter	description	**range min-max of values from literature**	**value 2 year life cycle 2x2-model**	**value 4 year life cycle 4x4-model**	**dimensio**
b	Number of days that eggs are laid (spawning season)	30-51[1]	30	30	d
w	Number of days that diapause (winter) lasts	135-255[2]	155	215	d
s_0	Daily survival throughout the first year of life	0.85-0.995[3]	0.9685	0.97	d^{-1}
s_1	Daily survival throughout the second year of life	0.851-0.97[3]	0.998	0.991	d^{-1}
s_2	Daily survival throughout the third year of life	0.851-0.94[3]	-	0.992	d^{-1}
s_3	Daily survival throughout remaining life (at age 3+)	0.851-0.94[3]	-	0.998	d^{-1}
m	The number of eggs laid per day per female in the spawning season	11-127[4]	47	47	No d^{-1}

[1]Hirche (1989); [2] Assuming diapause length is 365 days minus length of growth season (reported growth season 3 to 6 months (120-180 days) (Ankvaern et al. (2005), Ji et al. (2012), Darnis & Fortier (2014)) and spawning season (30 days); [3] Ankvaern et al. (2005), Thor et al. (2008); [4] Melle & Skjoldal (1998), Niehoff et al., (2002), Niehoff & Hirche (2005), Hirche (2013)

***Table 2*:** Elasticity and sensitivity of (a) the 2x2 and (b) the 4x4 matrix model

(a)

parameter	value	sensitivity	elasticity
s_0	0.9685	61.8	58.5
s_1	0.998	155	151
m	47	0.0057	0.26
b	30	0.0055	0.16
w	155	0.01	1.53

(b)

parameter	value	sensitivity	elasticity
s_0	0.970	25.31	24.21
s_1	0.991	22.88	22.36
s_2	0.992	22.86	22.36
s_3	0.998	82.37	81.07
m	47	0.0032	0.15
b	30	0.003	0.09
w	215	0.008	1.76

Table 3: Toxic Units (TU) based on real, experimental (exp.) and model simulated (mod.) oil spills in the (sub)Arctic. The derivation of these TU can be found in ESM1 section 4.

Type	Location	Release	Spill size (m^3 crude oil)	Treatment of oil	Substances	TU	Ref.
Exp.	Barents Sea	Water surface	7	Untreated	Dissolved hydrocarbons	0.003 -0.05	1
					Total hydrocarbons	0.001 - 0.008	
Real	Prince William Sound	Water surface	~45,000	Untreated	TPAH	0.00003 - 1.40 (mean 0.002)	2
Mod.	Beaufort Sea	Blow-out, subsurface release during 30-120 days	Max 2,009,000,000	Untreated	Dissolved aromatic hydrocarbons	0.03 - 6.25	3
				Dispersant application	Dissolved aromatic hydrocarbons	0.03 - 15.63	

[a]: northern Gulf of Alaska; 1) Faksness et al. (2011); 2) Boehm et al. (2007); 3) Schroeder Gearon et al. (2014)

Figures

(a) (b)

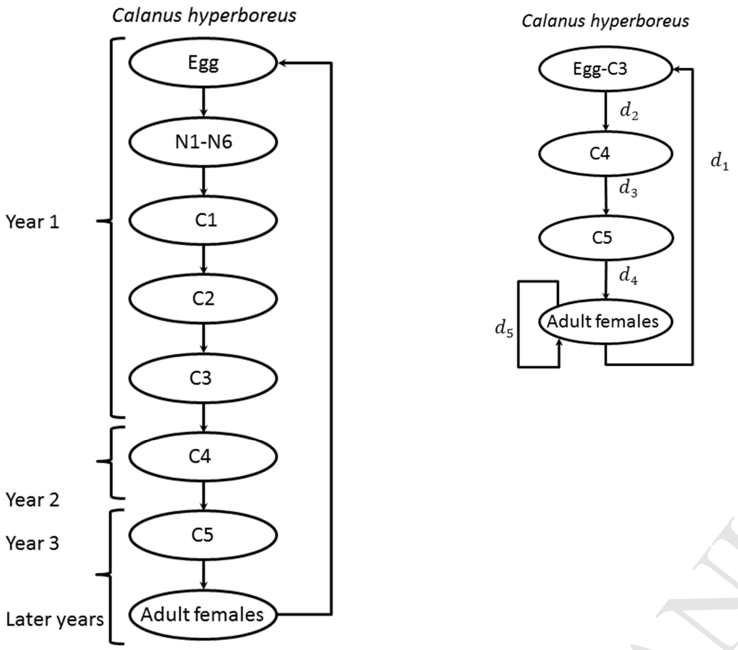


Figure 1: the real (panel a) and modelled (panel b) life cycle with generation time of four years for *C. hyperboreus*. N1-N6: nauplii stages 1-6; C1-C5: copepodite stages 1-5; d_1: reproductive value; d_2: survival to C4; d_3: survival to C5; d_4: survival to adult female (using a sex ratio 1:1) and d_5: yearly survival of adult females.

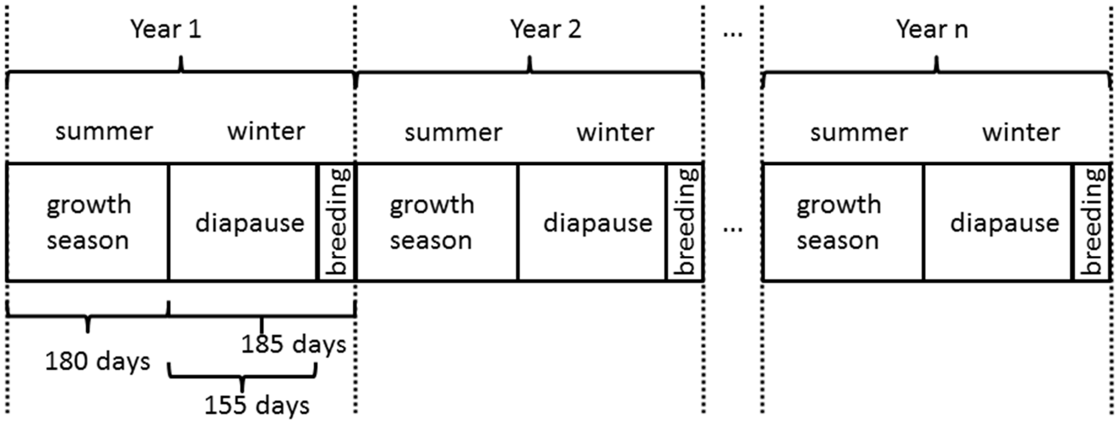
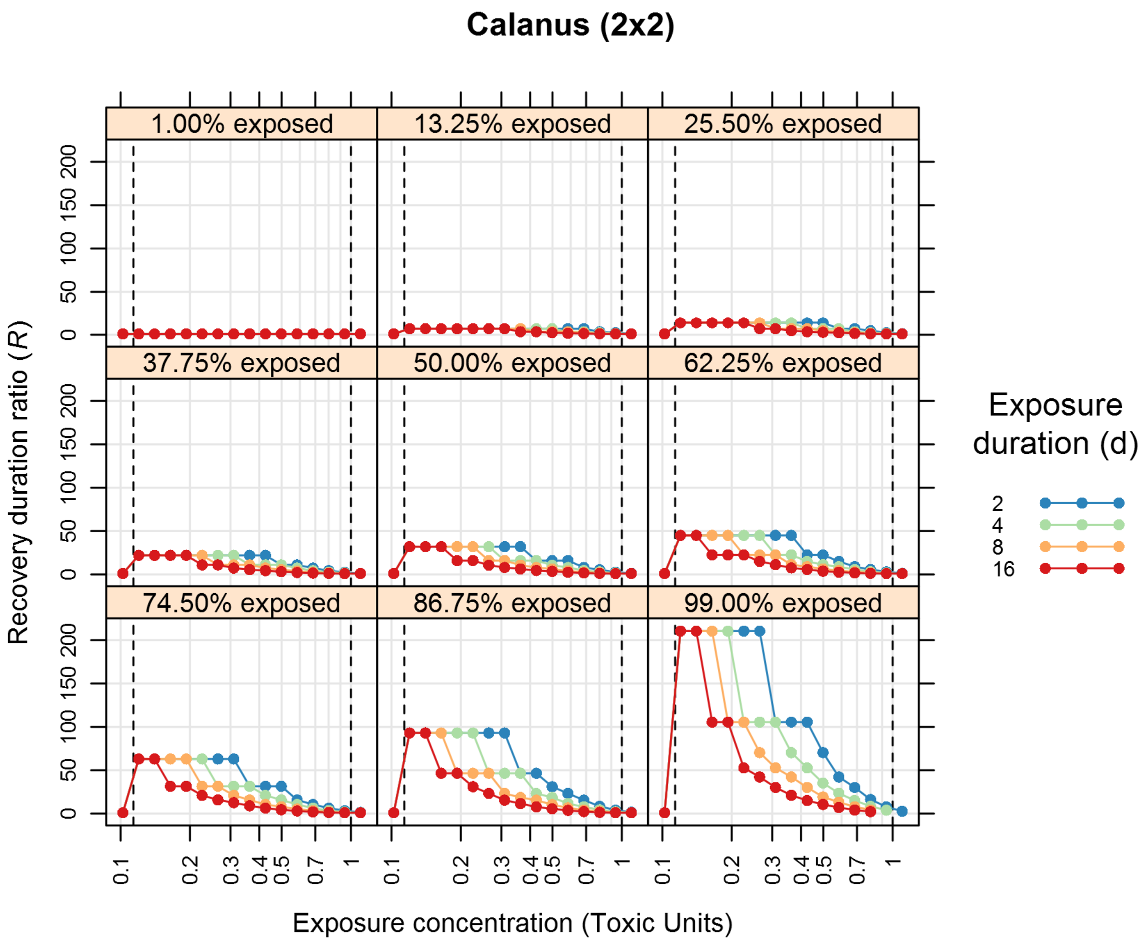
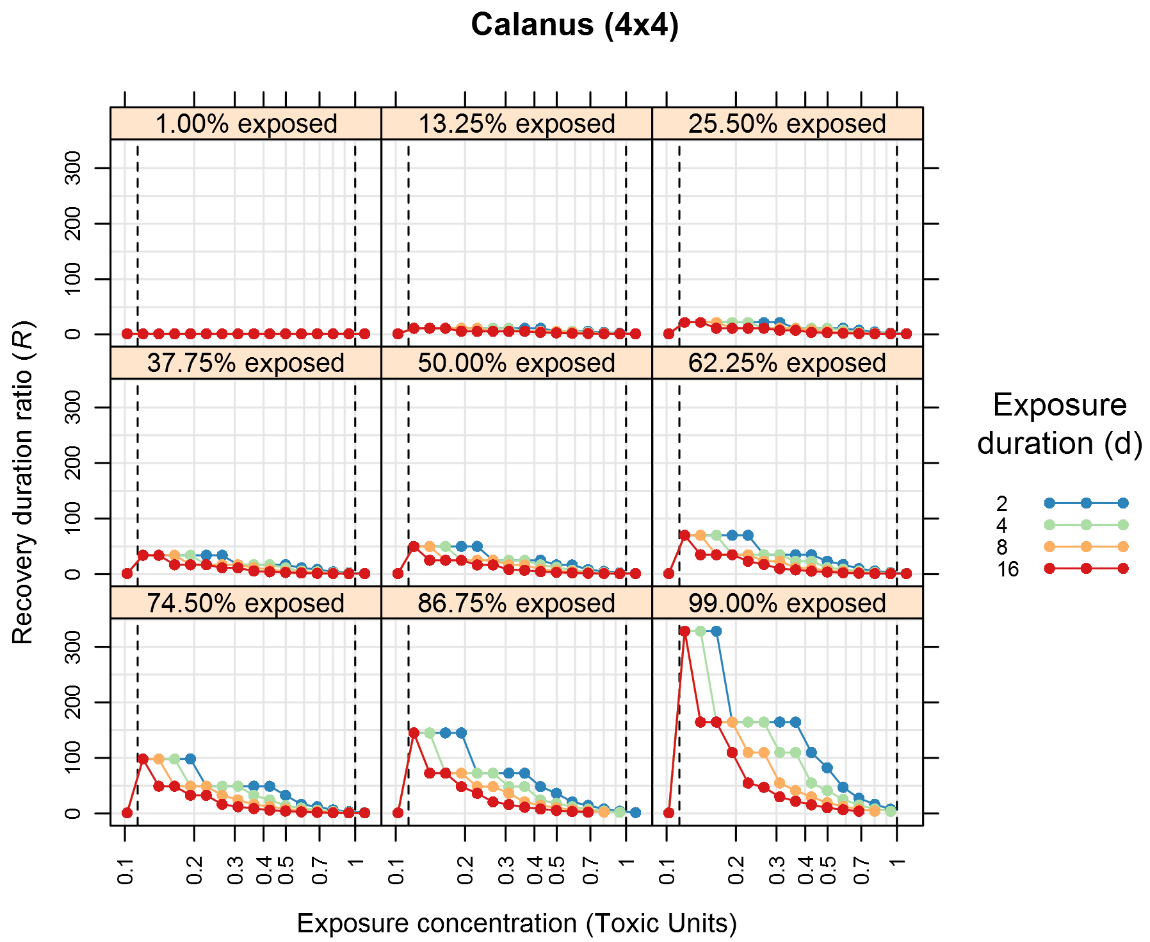


Figure 2: the year as modelled for *C. hyperboreus* life cycle with a generation time of two years.


Calanus (2x2)
1.00% exposed
13.25% exposed
25.50% exposed
37.75% exposed
50.00% exposed
62.25% exposed
74.50% exposed
86.75% exposed
99.00% exposed
Recovery duration ratio (R)
0 50 100 150 200
0.1 0.2 0.3 0.4 0.5 0.7 1
Exposure concentration (Toxic Units)
Exposure duration (d)
2
4
8
16

721 **A**



B

Figure 3: The ratio *R* (eqn 5) between the precautionary approach (=worst case scenario) and the refined approach is shown for the Calanus 2x2 model (A) and 4x4 model (B). In 9 panels the percentage exposed is increased linearly from 1 to 99%, see the header of each panel. The ratio *R* is given as a function of the exposure concentration and the duration of the exposure (denoted with different coloured lines). The left-dashed vertical line resembles the NOEC (n=1/ACR in TU) and the right-dashed vertical line the LC50 (L=1 in TU). The minimum recovery duration is one year. The ratio *R* is equal to 1 when the precautionary approach and the refined approach result in the same recovery duration, when *R* is greater than 1, recovery times calculated with the precautionary approach are longer than those calculated with the refined approach. The curves are not smooth, because the recovery durations (used to calculate R) are expressed as full years.

ESM1: Supplementary information

1. Development and analysis of the 4x4 model for *C. hyperboreus*

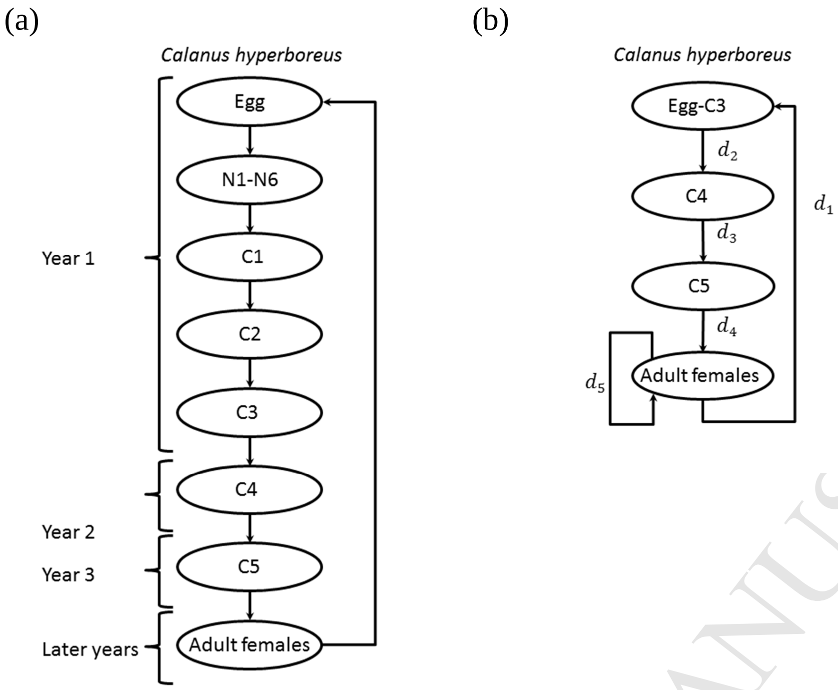


Figure S.1: the real (panel a) and modelled (panel b) life cycle with generation time of four years for *C. hyperboreus*. Note that only females are considered in the model. N1-N6: nauplius stages 1-6; C1-C5: copepodite stages 1-5; d_1: reproductive value; d_2: survival to C4; d_3: survival to C5; d_4: survival to adult female and d_5: yearly survival of adult females.

In some parts of the Arctic the life cycle of *Calanus hyperboreus* lasts 3 or more years. In those areas the development in the first year of the life of this Crustacean species starts with the egg stage (50% is assumed female), via six nauplius stages up to the third copepodite stage. The next two copepodite stages both last a full year. Thereafter the individuals become mature adults. Because we only consider females in the model, this stage is called adult females.

The 4x4-model is represented in figure S.1b and based on the real life cycle (given in Fig. S.1a). Thus, for the model with a generation time of four years the four classes $(x_0(t), x_1(t), x_2(t), x_3(t))^T$ represent the just born *Calanus* (0+ to one year old), 1+ to two years old, 2+ to three years old and older than three years. The Leslie matrix for this system (figure 1b) only has positive values on the places marked with a symbol (see equation 1; note that the time τ is measured in years). How these positive values are derived from daily-based rates and what they look like in terms of daily survival and fecundity, is explained in the section “from days to year” (below).

$$\begin{pmatrix} x_0(\tau+1) \\ x_1(\tau+1) \\ x_2(\tau+1) \\ x_3(\tau+1) \end{pmatrix} = \begin{pmatrix} 0 & 0 & 0 & d_1 \\ d_2 & 0 & 0 & 0 \\ 0 & d_3 & 0 & 0 \\ 0 & 0 & d_4 & d_5 \end{pmatrix} \begin{pmatrix} x_0(\tau) \\ x_1(\tau) \\ x_2(\tau) \\ x_3(\tau) \end{pmatrix} \quad \text{eqn S.1}$$

Based on data from the life cycle of *C. hyperboreus* we have to consider that these crustaceans do have a diapause period during the year, namely when they have migrated into the deep. We assumed that in this period no mortality and reproduction takes place (Fig S.2).

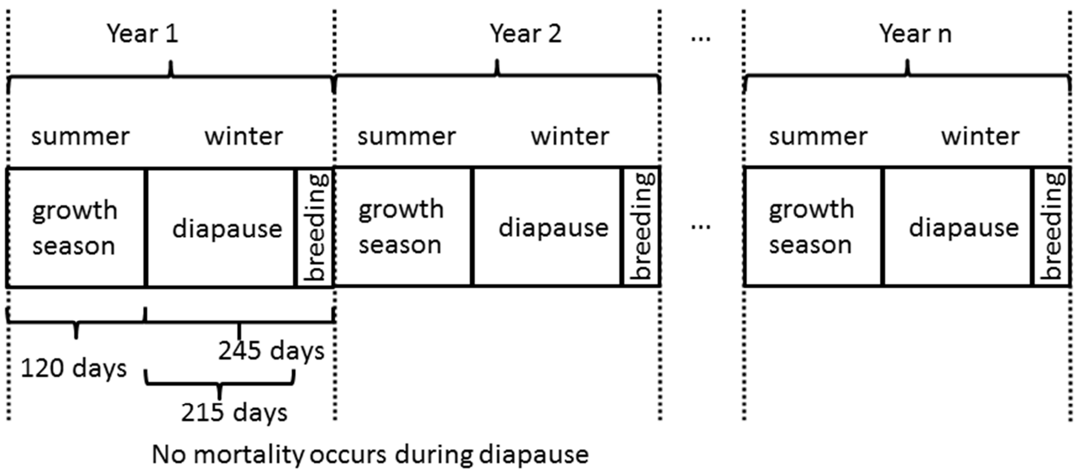


Figure S.2: the year as modelled for *C. hyperboreus* life cycle with a generation time of four years.

From days to year

Assume that diapause lasts w days and the spawning season lasts b days. We start to model just after the spawning season, because we model post-spawning. Then we have $365 - w - b$ days during which for the four classes only the daily survival probabilities should be accounted for. The daily survival probabilities are respectively s_0, s_1, s_2 and s_3. For those days equation A.1 holds, here the time t is given in days.

$$\begin{pmatrix} x_0(t+1) \\ x_1(t+1) \\ x_2(t+1) \\ x_3(t+1) \end{pmatrix} = \begin{pmatrix} s_0 & 0 & 0 & 0 \\ 0 & s_1 & 0 & 0 \\ 0 & 0 & s_2 & 0 \\ 0 & 0 & 0 & s_3 \end{pmatrix} \begin{pmatrix} x_0(t) \\ x_1(t) \\ x_2(t) \\ x_3(t) \end{pmatrix} \quad \text{for } t = 1, \ldots, (365 - w - b) \qquad \text{eqn S.1}$$

Accounting for diapause in which everyone survives gives eqn. S.2

$$\begin{pmatrix} x_0(t+1) \\ x_1(t+1) \\ x_2(t+1) \\ x_3(t+1) \end{pmatrix} = \begin{pmatrix} 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \end{pmatrix} \begin{pmatrix} x_0(t) \\ x_1(t) \\ x_2(t) \\ x_3(t) \end{pmatrix} \quad \text{for } t = (366 - w - b), \ldots, (365 - b) \qquad \text{eqn S.2}$$

Because the matrix is the identity matrix during this period, this period is not accounted for in the product matrix that considers the full year. Only adults reproduce, and the newborn female *Calanus* sp. are temporarily stored in the variable $y(t)$. For the first day of the spawning season we have to create this temporary variable:

$$\begin{pmatrix} y(t+1) \\ x_0(t+1) \\ x_1(t+1) \\ x_2(t+1) \\ x_3(t+1) \end{pmatrix} = \begin{pmatrix} 0 & 0 & 0 & \frac{m}{2} s_3 \\ s_0 & 0 & 0 & 0 \\ 0 & s_1 & 0 & 0 \\ 0 & 0 & s_2 & 0 \\ 0 & 0 & 0 & s_3 \end{pmatrix} \begin{pmatrix} x_0(t) \\ x_1(t) \\ x_2(t) \\ x_3(t) \end{pmatrix} \quad \text{for } t = 366 - b \qquad \text{eqn S.3}$$

Subsequently the spawning season lasts for $b - 1$ days:

$$\begin{pmatrix} y(t+1) \\ x_0(t+1) \\ x_1(t+1) \\ x_2(t+1) \\ x_3(t+1) \end{pmatrix} = \begin{pmatrix} s_0 & 0 & 0 & 0 & \frac{m}{2} s_3 \\ 0 & s_0 & 0 & 0 & 0 \\ 0 & 0 & s_1 & 0 & 0 \\ 0 & 0 & 0 & s_2 & 0 \\ 0 & 0 & 0 & 0 & s_3 \end{pmatrix} \begin{pmatrix} y(t) \\ x_0(t) \\ x_1(t) \\ x_2(t) \\ x_3(t) \end{pmatrix} \quad \text{for } t = (367 - b), \ldots, 365 \qquad \text{eqn S.4}$$

Just after the spawning season we have to return to the original four classes:

$$\begin{pmatrix} x_0(t+365) \\ x_1(t+365) \\ x_2(t+365) \\ x_3(t+365) \end{pmatrix} = \begin{pmatrix} 1 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 1 & 1 \end{pmatrix} \begin{pmatrix} y(t+365^-) \\ x_0(t+365^-) \\ x_1(t+365^-) \\ x_2(t+365^-) \\ x_3(t+365^-) \end{pmatrix} \qquad \text{eqn S.5}$$

In total the year-to-year matrix, with time τ represented in years, is:

$$\begin{pmatrix} x_0(\tau+1) \\ x_1(\tau+1) \\ x_2(\tau+1) \\ x_3(\tau+1) \end{pmatrix} = \begin{pmatrix} 0 & 0 & 0 & \frac{m}{2} s_3^{366-b-w}\left(\frac{s_0{}^b - s_3{}^b}{s_0 - s_3}\right) \\ s_0{}^{365-w} & 0 & 0 & 0 \\ 0 & s_1{}^{365-w} & 0 & 0 \\ 0 & 0 & s_2{}^{365-w} & s_3{}^{365-w} \end{pmatrix} \begin{pmatrix} x_0(\tau) \\ x_1(\tau) \\ x_2(\tau) \\ x_3(\tau) \end{pmatrix} = L \begin{pmatrix} x_0(\tau) \\ x_1(\tau) \\ x_2(\tau) \\ x_3(\tau) \end{pmatrix} \qquad \text{eqn S.6}$$

Elasticities:

The characteristic equation for matrix *L* is:

$$\lambda^4 - s_3{}^{365-w}\lambda^3 - \frac{m}{2}(s_0 s_1 s_2 s_3)^{365-w} s_3{}^{1-b}\left(\frac{s_0{}^b - s_3{}^b}{s_0 - s_3}\right) = 0 \qquad \text{eqn S.7}$$

The dominant eigenvalue of this characteristic equation can only be calculated numerically and when the dominant eigenvalue is known for particular parameter values, the elasticities (or relative sensitivities) can be calculated using the analytic expressions below (derived via implicit differentiation of the characteristic equation), for the elasticity of parameter *b* (eqn S.8), parameter s_0 (eqn S.9), parameter s_1 (eqn S.10), parameter s_2 (eqn S.11), parameter s_3 (eqn S.12) parameter *m* (eqn S.13) and parameter *w* (eqn S.14).

$$e(b) = \frac{b}{\lambda}\frac{\partial \lambda}{\partial b} == \frac{\frac{bm}{2}\log\left(\frac{s_0}{s_3}\right)(s_0 s_1 s_2 s_3)^{365-w} s_3\left(\frac{s_0}{s_3}\right)^b}{\left(4\lambda^4 - 3\lambda^3 s_3{}^{365-w}\right)(s_0 - s_3)} \qquad \text{eqn. S.8}$$

$$e(s_0) = \frac{s_0}{\lambda}\frac{\partial\lambda}{\partial s_0} = \frac{\frac{m}{2}\left(s_0 s_1 s_2 s_3\right)^{365-w}\left(\left((365-w+b)\left(\frac{s_0}{s_3}\right)^{b-1} - (365-w)\left(\frac{s_0}{s_3}\right)^{-1}\right)\left(s_0 - s_3\right) - s_3\left(\left(\frac{s_0}{s_3}\right)^{b} - 1\right)\right)}{\left(4\lambda^4 - 3\lambda^3 s_3{}^{365-w}\right)\left(s_0 - s_3\right)^2} \qquad \text{eqn S.9}$$

$$e(s_1) = \frac{s_1}{\lambda}\frac{\partial\lambda}{\partial s_1} = \frac{\frac{m}{2}(365-w)\left(s_0 s_1 s_2 s_3\right)^{365-w} s_3\left(\left(\frac{s_0}{s_3}\right)^{b} - 1\right)}{\left(4\lambda^4 - 3\lambda^3 s_3{}^{365-w}\right)\left(s_0 - s_3\right)} \qquad \text{eqn S.10}$$

$$e(s_2) = \frac{s_2}{\lambda}\frac{\partial\lambda}{\partial s_2} = \frac{\frac{m}{2}(365-w)\left(s_0 s_1 s_2 s_3\right)^{365-w} s_3\left(\left(\frac{s_0}{s_3}\right)^{b} - 1\right)}{\left(4\lambda^4 - 3\lambda^3 s_3{}^{365-w}\right)\left(s_0 - s_3\right)} \qquad \text{eqn S.11}$$

$$e(s_3) = \frac{s_3}{\lambda}\frac{\partial\lambda}{\partial s_3} = \frac{(365-w)\, s_3{}^{365-w}}{\left(4\lambda - 3 s_3{}^{365-w}\right)} + \frac{\frac{m}{2} s_3\left(s_0 s_1 s_2 s_3\right)^{365-w}\left(w - 366 - (366-w-b)\left(\frac{s_0}{s_3}\right)^{b} + s_3\left(\left(\frac{s_0}{s_3}\right)^{b} - 1\right)\right)}{\left(4\lambda^4 - 3\lambda^3 s_3{}^{365-w}\right)\left(s_0 - s_3\right)^2} \qquad \text{eqn S.12}$$

$$e(m) = \frac{m}{\lambda}\frac{\partial\lambda}{\partial m} = \frac{\frac{m}{2}\left(s_0 s_1 s_2 s_3\right)^{365-w} s_3\left(\left(\frac{s_0}{s_3}\right)^{b} - 1\right)}{\left(4\lambda^4 - 3\lambda^3 s_3{}^{365-w}\right)\left(s_0 - s_3\right)} \qquad \text{eqn S.13}$$

$$e(w) = \frac{w}{\lambda}\frac{\partial\lambda}{\partial w} = \frac{-w\ln(s_3)\, s_3{}^{365-w}}{\left(4\lambda - 3 s_3{}^{365-w}\right)} - \frac{w\ln(s_0 s_1 s_2 s_3)\frac{m}{2}\left(s_0 s_1 s_2 s_3\right)^{365-w} s_3\left(\left(\frac{s_0}{s_3}\right)^{b} - 1\right)}{\left(4\lambda^4 - 3\lambda^3 s_3{}^{365-w}\right)\left(s_0 - s_3\right)} \qquad \text{eqn S.14}$$

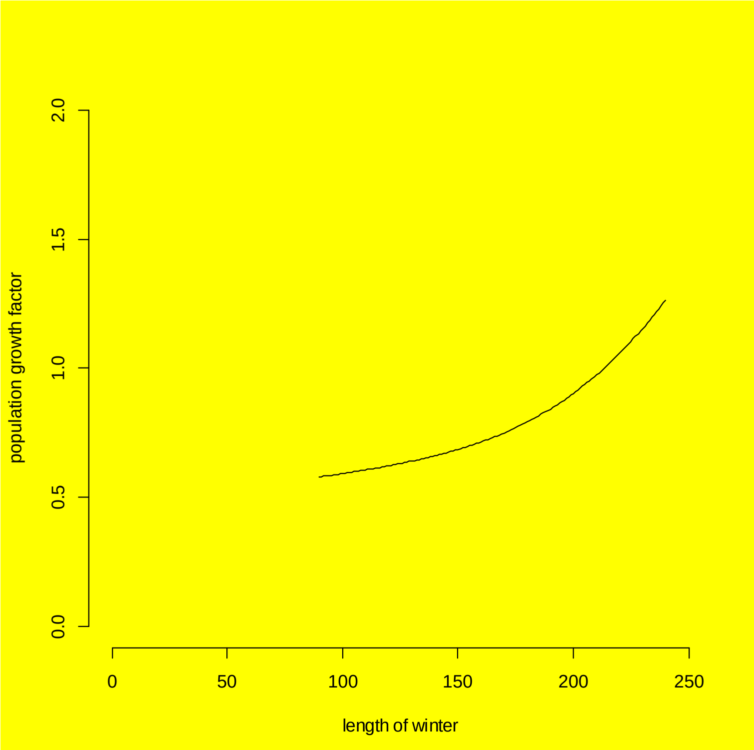


Figure S.3: The influence of the length of the winter *w* on the population growth factor in the 4x4 model. It should be noted that when the winter lasts longer then the modelled population has a longer time period without mortality and thus the population growth factor increases with *w*.

2. Detailed description of literature data for *Calanus*.

Reproduction

In the field, the egg production rate of *Calanus* varies during the active season, depending on for example the food supply (*C. glacialis* , Melle and Skjoldal (1998)). During the algal bloom in the polar front region of the Barents Sea the egg production of *C. glacialis* ranged from 17 to 77 eggs d^{-1} per female in April, whereas average reproduction values are respectively 22 and 11 eggs d^{-1} per female in March respectively May-July (Melle and Skjoldal 1998). Lower values were observed in the field by Daase et al. (2013), namely a maximum of 18-23 eggs per week for *C. glacialis* across the Arctic. However, such low rates have not been reported by other studies. Laboratory experiments conducted at 0 °C with female *C. glacialis* collected from the East Greenland Current in June of 1987 and 1988 showed egg production rates of 29 ± 31 (mean ± s.d.) and 42 ± 38 eggs d^{-1} per female, respectively (Hirche 1989). More than half of the females were laying eggs during 30 to 35 d, while 20% was actively spawning for up to 51 d. In the Lurefjord (western Norway) Niehoff and Hirche (2005) observed a maximum egg production rate for *C. glacialis* in March of 36 eggs d^{-1} per female and a range of 18-112 eggs d^{-1} per female for *C. glacialis* at different locations in the Arctic was reported. For *C. hyperboreus* reported egg production values are between 1,000 and 3,800 eggs per year per *C. hyperboreus* female (Hirche 2013). Calculated values for *Calanus species*, based on the observed rates by Melle and Skjoldal (1998) and egg production rates of *Calanus* species in Disko Bay, West Greenland were similar (Niehoff et al. 2002): 33 eggs d^{-1} per *C. hyperboreus* female (March) and 40 eggs d^{-1} per *C. glacialis* female (May).

Active season

Field observations in Billefjorden, Spitsbergen (Ankvaern et al. 2005) showed a sharp increase in abundance (ind m^{-2}) of *C. glacialis* and *C. hyperboreus* in May with peaks in June (*C. hyperboreus*) and July (*C. glacialis*). Copepods, recruited from new-borns and surfacing overwintering adults, were found in the pelagic from March (*C. hyperboreus*) respectively May (*C. glacialis*) until August. They remained in the pelagic for 6 months (*C. hyperboreus*), respectively 4 months (*C. glacialis*) and during this period reproduction take place. The reproductive period coincides with the algal bloom. Modelling results of Ji et al. (2012) indicate that the length of the algal bloom ranges from approximately 80 to 150 days based on chlorophyll concentrations and about 150 to 200 days based on snowmelt, for the north and south of Spitsbergen, respectively. The observed growth season length of ca.150 days fits these calculations. Darnis and Fortier (2014) investigated the seasonal vertical migration of dominant arctic copepod species (*C. hyperboreus*) in Amundsen Gulf, Beaufort Sea. This spec. resides in the deep Atlantic Layer from December to mid-April, rapidly invades the surface layer at the onset of the phytoplankton bloom in early May, and started its descent to overwintering depth in July. In contrast *C. glacialis* overwinters at shallower depths than *C. hyperboreus* and moves into the surface layer in early April as ice algae bloom, and remains in the subsurface until the end of July. Although diapause at depth during winter is a common observed strategy for *Calanus* (e.g. Ankvaern et al. 2005; Darnis and Fortier 2014; Falk-Petersen 2009), there are also observations of *Calanus spp*. in the surface water layers during winter, suggesting they may be more active during winter than often assumed (Daase et al. 2014; Berge et al., 2015; Blachowiak-Samolyk et al., 2015). In summary, the growth season lengths found in literature for *C. glacialis* equalled 4 months in the Beaufort Sea (Darnis and Fortier 2014) and Billefjorden, Spitsbergen (Ankvaern et al. 2005) and for *C. hyperboreus* it ranges from 3 months in the Beaufort Sea (Darnis and Fortier 2014) to 6 months in Billefjorden, Spitsbergen (Ankvaern et al. 2005). Based on these data a yearly growth season of approximately 4 months was used for *C. glacialis* and 4 or 6 months for *C. hyperboreus* in our models.

Mortality

Natural mortality of *Calanus* in the Arctic is caused by predation, starvation, environmental conditions, and parasitic or viral infection (Daase et al. 2014). Mortality constants for the various life stages are site and time specific making mortality estimation very complex (Melle and Skjoldal 1998).

Hatching success for *C. hyperboreus* was 75-98% (Jung-Madsen et al. 2013) and for *C. glacialis* 75-86% (Weydmann et al. 2015). Mortality rates for nauplii are in the range of 0.04 and 0.09 d^{-1} for *C. hyperboreus* (Jung-Madsen et al. 2013) and 0.04 and 0.06 d^{-1} for *C. glacialis* (Daase et al. 2011; Jung-Madsen and Nielsen 2015). Because both studies note that the mortality rates are high, these values are probably not representative for a natural population.

Relative mortality rates for copepod stages in the field are estimated by Ankvaern et al. (2005) in Billefjorden, Spitsbergen, during March-July at ambient temperatures as approximately 0.01 (C1), 0.02 (C2), 0.04 (C3), 0.06 (C4), 0.12 (C5) and 0.15 (adult females) d^{-1} for *C. hyperboreus*. In the same study relative mortality rates estimated for *C. glacialis* were lower, namely approximately 0.005 (C1 and C2), 0.015 (C3), 0.03 (C4), 0.08 (C5) and 0.06 (adult females) d^{-1}. Thor et al. (2008) investigated relative mortality rates of copepods (stages C1-C5) in Disko Bay, western Greenland, during June 2001. Reported values for *C. hyperboreus* were approximately 0.005 (C1 & C2), 0.06 (C3), 0.08 (C4) and 0.06 (C5) d^{-1}, and for *C. glacialis* 0.1 (C1), 0.13 (C2), 0.15 (C3) and 0.06 d^{-1} (C5) (Thor et al. 2008). No value for C4 was reported. Both studies mention that the mortality rates are high and that this was probably caused by predation (Ankvaern et al. 2005; Thor et al. 2008). Both the mortality values for the copepod stages based on field observations and the estimates for the nauplius stages from laboratory experiments can only be used as an indication because of the high variability in ambient conditions throughout the Arctic Ocean.

References

Arnkværn G, Daase M, Eiane K (2005) Dynamics of coexisting *Calanus finmarchicus*, *Calanus glacialis* and *Calanus hyperboreus* populations in a high-Arctic fjord. Polar Biol 28: 528–538

Berge, J., Daase, M., Renaud, P.E., Ambrose, W.G., Darnis, G., Last, K.S. et al. (2015) Unexpected Levels of Biological Activity during the Polar Night Offer New Perspectives on a Warming Arctic. Curr. Biol. 25, 2555-2561.

Blachowiak-Samolyk, K., Wiktor, J. M., Hegseth, E. N., Wold, A., Falk-Petersen, S., Kubiszyn, A. M. (2015) Winter Tales: the dark side of planktonic life. Polar. Biol. 38, 23-36.

Daase M, Falk-Petersen S, Varpe Ø, Darnis G, Søreide JE, Wold A, Leu E, Berge J, Philippe B, Fortier L (2013) Timing of reproductive events in the marine copepod *Calanus glacialis*: a pan-Arctic perspective. Can J Fish Aquat Sci 70: 871-884

Daase M, Søreide JE, Martynova D (2011) Effects of food quality on naupliar development in *Calanus glacialis* at subzero temperatures. Mar Ecol Prog Ser 429: 111–124

Daase, M., Varpe, Ø., Falk-Petersen, S. (2014). Non-consumptive mortality in copepods: occurrence of *Calanus* spp. carcasses in the Arctic Ocean during winter. J. Plankton Res. 36, 129-144

Darnis G, Fortier L (2014) Temperature, food and the seasonal vertical migration of key arctic copepods in the thermally stratified Amundsen Gulf (Beaufort Sea, Arctic Ocean) J Plankton Res 36: 1092–1108

Falk-Petersen, S, Mayzaud P, Kattner G, Sargent JR (2009) Lipids and life strategy of Arctic *Calanus*. Mar Biol Res 5: 18–39

Hirche HJ (1989) Egg production of the Arctic copepod *Calanus glacialis*: laboratory experiments. Mar Biol 103: 311 -318

Hirche HJ (2013) Long-term experiments on lifespan, reproductive activity and timing of reproduction in the Arctic copepod *Calanus hyperboreus*. Mar Biol 160: 2469–2481

Ji RB, Ashjian CJ, Campbell RG, Chen CS, Gao GP, Davis CS, Cowles GW, Beardsley RC (2012) Life history and biogeography of *Calanus* copepods in the Arctic Ocean: An individual-based modeling study. Prog Oceanogr 96: 40–56

Jung-Madsen S and Nielsen TG (2015) Early development of *Calanus glacialis* and *C. finmarchicus*. Limnol Oceanogr 60 (3): 934-946

Jung-Madsen S, Nielsen TG, Grønkjær P, Hansen BW, Møller EF (2013) Early development of *Calanus hyperboreus* nauplii: Response to a changing ocean. Limnol Oceanogr 58: 2109–2121

Melle W, Skjoldal HR (1998) Reproduction and development of *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus* in the Barents Sea. Mar Ecol Prog Ser 169: 211–228

Niehoff B, Hirche HJ (2005) Reproduction of *Calanus glacialis* in the Lurefjord (western Norway): indication for temperature-induced female dormancy. Mar Ecol Prog Ser 285: 107–115

Niehoff B, Madsen SD, Hansen BW, Nielsen TG (2002) Reproductive cycles of three dominant *Calanus* species in Disko Bay, West Greenland. Mar Biol 140: 567–576

Thor P, Nielsen TG, Tiselius P (2008) Mortality rates of epipelagic copepods in the post-spring bloom period in Disko Bay, western Greenland. Mar Ecol Prog Ser 359: 151–160

Weydmann A, Zwolicki A, Muś K, Kwaśniewski S (2015) The effect of temperature on egg development rate and hatching success in *Calanus glacialis* and *C. finmarchicus.* Polar Res 34. doi:10.3402/polar.v34.23947

3. Exact solution for the precautionary approach (eqn 4 in main text)

In the assumption that the population is at its stable age distribution the dominant eigenvalue λ is the yearly population growth factor and the years to recovery T_r is based on growth from f to 1. f is in this case both the fraction of killed individuals as well as the exposed fraction of individuals (i.e., the precautionary approach from the main text). We arrive at:

$$\lambda^{T_r} = \frac{1}{f} \qquad \text{eqn S.21}$$

Which can be solved by:

$$T_r = \frac{-\log(f)}{\log(\lambda)} \qquad \text{eqn S.22}$$

For comparability with simulation results, the solution needs to be rounded to its integer ceiling (indicated by the double rectangular brackets):

$$T_r = \left[\left[\frac{-\log(1-f)}{\log(\lambda)}\right]\right] \qquad \text{eqn S.22}$$

4. Derivation of field relevant Toxic Units

In our study we used TU to express exposure concentrations. The TU range applied in this study increases up to 1.1, which corresponds to an exposure concentration that is 10% above the LC50. Exposure above LC50 values can be realistic in field situations, especially directly after and/or near the source of a spill. After the Exxon Valdez oil spill in 1989 (located in Prince William Sound, a subarctic fjord-type embayment of the northern Gulf of Alaska) 1288 water samples were taken along the spill path in that same year (Boehm et al. 2007). The highest measured concentration of total poly-aromatic hydrocarbons (TPAH) was 42 ppb (range <0.001-42, mean 0.058 ppb) with only 9 samples containing more than 10 ppb TPAH, which is the State of Alaska’s water-quality standard for total aromatic hydrocarbons (Boehm et al. 2007). Taking the LC50 value for *C. glacialis* exposed to mechanically dispersed oil of 30 ppb total PAH (Gardiner et al. 2013, see Table S.1) this relates to a TU between a small value of less than 0.00003 and a maximum of 1.40 (mean: 0.002). A field experiment in the Barents Sea (where crude oil was released between the ice floes and was left untreated to study oil weathering and spreading in ice) showed lower concentrations of oil, ranging between 0.1 and 1.5 ppb dissolved hydrocarbons and 4-32 ppb total hydrocarbons (Faksness et al. 2011). The water soluble fraction was dominated by PAHs. For total hydrocarbons this relates to a TU ranging between 0.001 and 0.008 (based on a LC50 value of the water accommodated fraction of oil after mechanical dispersion: 4000 ppb total petroleum hydrocarbon (Gardiner et al. 2013). The toxicity of the water soluble fraction of oil has been studied for *Calanus* spp. (Jensen and Carroll 2010), but LC50 values were not determined. Therefore, we take the concentration of dissolved PAH, 3.6 ppb, at which no effects on egg hatching and egg production for *Calanus* spp. were observed (Jensen and Carroll 2010) and calculate the LC50 using the ACR of 8.8 (May et al. 2016) to be 32 ppb. With these assumptions, this relates to a TU between 0.003 and 0.05. Besides actual spill concentrations and experimental spill concentrations, as described above, our results can also be compared to concentrations from oil spill modelling. Multiple types of oil spill scenarios that could occur in the Beaufort Sea have been analysed (Schroeder Gearon et al. 2014). Dissolved aromatic concentrations ranged between 1 and 100 ppb, with some occasional spikes of up to 200 ppb within max 250-500 km of the spill site (Schroeder Gearon et al. 2014). In some cases dissolved aromatics could persist up to 30 days after the end of the release. Subsurface dispersant response often resulted in dissolved aromatic concentrations between 100 and 500 ppb (Schroeder Gearon et al. 2014). LC50 values for aromatics have not been found in the literature. Aromatics refer to both mono-aromatics (the highly volatile compounds benzene, xylene etc.) and poly-aromatics (i.e. PAHs). Assuming that the modelled concentration of dissolved aromatics are mainly PAHs (as the monocyclic compounds rapidly evaporate), this relates to TUs between 0.03 and 6.25 for untreated oil and between 0.03 and 15.63 for chemically dispersed oil (based on the calculated LC50 for dissolved petroleum compounds, see above, and disregarding the effect of dispersants on the toxicity of oil). In summary, TUs in field situations range between small values less than 0.00003 and 15.63, with most values below 0.1 TU.

Table S.1 Toxicity data available from literature for C. glacialis

Exposed to	**Effect**	**Duratio**	**Effect value**	**Unit**	**Reference**
Artificial produced water	EC50 (survival)	96 h	5.25 ± 2.20	fraction of the undiluted produced water	Camus et al.
	NEC	96 h	0.23 ± 0.14	fraction of the undiluted produced water	Camus et al.
Chemically dispersed oil	LC50	12 d	22 ± 9.5*	mg/l, petroleum hydrocarbon	Gardiner et a
	LC50	12 d	30-75**	mg/l, petroleum hydrocarbon	Gardiner et a
	LC50	12 d	0.06 ± 0.03*	mg/l, total PAH	Gardiner et a
	LC50	12 d	0.13 ± 0.08**	mg/l, total PAH	Gardiner et a
	LC50	12 d	0.026 ± 0.016*	mg/l, naphthalene	Gardiner et a
	LC50	12 d	0.054 ± 0.031**	mg/l, naphthalene	Gardiner et a
Mechanically dispersed oil	LC50	12 d	4.0 ± 1.1*	mg/l, petroleum hydrocarbon	Gardiner et a
	LC50	12 d	0.03 ± 0.01*	mg/l, total PAH	Gardiner et a
	LC50	12 d	0.05 ± 0.034*	mg/l, naphthalene	Gardiner et a
Water	LC50	96 h	1.037	µg THC/L	Hansen et al
Water soluble fraction (WSF) of oil	LOEC (reduced	12 d	10.4	µg /l, PAH (16-EPA)	Jensen and C
	NOEC (egg	12 d	3.6	µg /l, PAH (16-EPA)	Jensen and C
	NOEC (egg	12 d	10.4	µg /l, PAH (16-EPA)	Jensen and C

EC50: the effective concentration at 50%, which is the concentration that causes adverse effects in 50% of the test organisms; LC50: the lethal concentration at 50%, which is the concentration that causes 50% of the test organisms to die; NEC: no effect concentration, which is the concentration that will not cause an effect to the test organisms; THC: Total hydrocarbon concentration; * Early open-water season; ** Late open-water season; # adult females were exposed during 12 days. Egg hatching success was examined during 2 days after the exposure treatment.

References

Boehm, P.D., Neff, J.M., Page, D.S. (2007) Assessment of polycyclic aromatic hydrocarbon exposure in the waters of Prince William Sound after the Exxon Valdez oil spill: 1989-2005. Marine Pollution Bulletin, 54 (3), pp. 339-356. DOI: 10.1016/j.marpolbul.2006.11.025

Camus L, Brooks S, Geraudie P, Hjorth M, Nahrgang J, Olsen GH, Smit MGD (2015) Comparison of produced water toxicity to Arctic and temperate species. Ecotoxicology and Environmental Safety 113(0): 248-258.

Faksness L.-G., Brandvik P.J., Daae R.L., Leirvik F., Børseth J.F. (2011) Large-scale oil-in-ice experiment in the Barents Sea: monitoring of oil in water and MetOcean interactions. Mar. Pollut. Bull., 62, pp. 976–984

Gardiner WW, Word JQ, Word JD, Perkins RA, Mcfarlin KM, Hester BW, Word LS, Ray CM (2013) The acute toxicity of chemically and physically dispersed crude oil to key arctic species under arctic conditions during the open water season. Environmental Toxicology and Chemistry, 32 (10), pp. 2284-2300. DOI: 10.1002/etc.2307

Hansen, B.H., Altin, D., Rorvik, S.F., Overjordet, I.B., Olsen, A.J., Nordtug, T., (2011) Comparative study on acute effects of water accommodated fractions of an artificially weathered crude oil on *Calanus finmarchicus* and *Calanus glacialis* (Crustacea: Copepoda). Science of the Total Environment 409, 704e709.

Jensen, L.K., Carroll, J. (2010) Experimental studies of reproduction and feeding for two Arctic-dwelling *Calanus* species exposed to crude oil. Aquatic Biology, 10 (3), pp. 261-271. DOI: 10.3354/ab00286

May M, Drost W, Germer S, Juffernholz T, Hahn S (2016) Evaluation of acute-to-chronic ratios of fish and *Daphnia* to predict acceptable no-effect levels. Environ Sci Eur 28: 16. doi:10.1186/s12302-016-0084-7

Schroeder Gearon M, French McCay D., Chaite E., Zamorski S., Reich D., Rowe J., Schmidt-Etkin D. (2014) SIMAP Modelling of Hypothetical Oil Spills in the Beaufort Sea for World Wildlife Fund (WWF). April 17, RPS Group plc Applied Science Associates and Environmental Research Consulting. South Kingstown, USA. http://awsassets.wwf.ca/downloads/wwf_beaufort_sea_oil_spill_modelling_full_report_rps_asa.pdf

Highlights

- Population models are set up for two Arctic *Calanus* spp.
- Toxic effects of oil on model parameters are included based on theoretical approach
- Recovery is compared using a precautionary and full dose-response approach
- Just above the NOEC the ratio between the two approaches can be more than 300
- This indicates the level of conservatism used in oil spill response