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Life cycle bioenergetics of the gray seal (*Halichoerus grypus*) in the Baltic Sea: Population response to environmental stress

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ABSTRACT

Wildlife population dynamics are shaped by multiple natural and anthropogenic factors, including predation, competition, stressful life history events, and external environmental stressors such as diseases and pollution. Marine mammals such as gray seals rely on extensive blubber layers for insulation and energy storage, making this tissue critical for survival and reproduction. This lipid rich blubber layer also accumulates hazardous fat soluble pollutants, such as polychlorinated biphenyls (PCBs), that can directly impact adipose function or be mobilized during periods of negative energy balance or transferred to offspring to exert further impacts on target tissues or vulnerable life stages. To predict how marine mammals will respond to ecological and anthropogenic stressors, it is necessary to use process-based modelling approaches that integrate environmental inputs, full species life history, and stressor impacts with individual dynamics of energy intake, storage, and utilization. The purpose of this study was to develop a full lifecycle dynamic energy budget and individual based model (DEB-IBM) that captured Baltic gray seal physiology and life history, and showcase potential applications of the model to predict population responses to select stressors known to threaten gray seals and other marine mammals around the world. We explore variations of three ecologically important stressors using phenomenological simulations: food limitation, endocrine disrupting chemicals that reduce fertility, and infectious disease. Using our calibrated DEB-IBM for Baltic gray seals, we found that continuous incremental food limitation can be more detrimental to population size than short random events of starvation, and further, that the effect of endocrine disruptors on population growth and structure is delayed due to bioaccumulation, and that communicable diseases significantly decrease population growth even when spillover events are relatively less frequent. One important finding is the delayed effect on population growth rate from some stressors, several years after the exposure period, resulting from a decline in somatic growth, increased age at maturation and decreased fecundity. Such delayed responses are ignored in current models of population viability and can be important in the correct assessment of population extinction risks. The model presented here provides a test bed on which effects of new hazardous substances and different scenarios of future environmental change affecting food availability and/or seal energetic demands can be investigated. Thus, the framework provides a tool for better understanding how diverse environmental stressors affect marine mammal populations and can be used to guide scientifically based management.

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1. Introduction

Wildlife population dynamics are shaped by multiple factors over evolutionary scales, including predation, competition, stressful life history events, and external environmental stressors such as diseases and habitat degradation (Darwin, 1859; Stenseth et al., 2004; Sæther and Engen, 2015). Many species across a wide range of ecosystems and landscapes have evolved in highly seasonal environments, often characterized by strong seasonal changes in environmental temperatures and food availability and quality (Leirs et al., 1997; Harrison et al., 2011). This is paired with the co-evolution with diseases and parasites and long-term fluctuations in climatological conditions (Näpflin et al., 2019). Furthermore, over the past century direct and indirect consequences of anthropogenic activities have significantly impacted wildlife populations. Given the ongoing trend of biodiversity loss and the complex interactions of ecological and anthropogenic stressors, wildlife managers urgently need qualified guidance and scientifically sound frameworks for implementing conservation actions.

Marine mammals are vulnerable to various anthropogenic stressors, including most notably food limitation, chemical pollution, and infectious diseases (Fair and Becker, 2000). Stress from food limitation can be caused by overfishing, climate/habitat change, disturbances at haul out sites, by-catch and hunting (Harding and Härkönen, 1999; McClenachan and Cooper, 2008; Edrén et al., 2010; Andersen et al., 2012, 2014; Sundqvist et al., 2012). Marine mammals are particularly susceptible to hazardous anthropogenic substances (HAS), since many environmental pollutants accumulate in lipid rich tissue, which is abundant and serves a critical role for these marine species. HAS, such as polychlorinated biphenyls (PCBs), organochlorine pesticides, and brominated and fluorinated flame retardants, have demonstrable effects on the physiology and health of exposed biota (e.g. Letcher et al., 2010). Furthermore, the adverse effects of HAS are compounded through interactions with other stressors. For instance, food limitation can cause mobilization of stored HAS in blubber and increase the risk of immune impacts on target immune tissues or circulating cell populations, thus increasing species susceptibility to infectious diseases and parasites (Ross et al., 1995; Hall et al., 1997; Reijnders et al., 2009; Desforges et al., 2016). The impact of such stressors is nowhere more apparent than in marine mammal populations in the Baltic Sea, particularly ringed (*Pusa hispida*) and gray seals (*Halichoerus grypus*). Baltic seal populations have experienced major fluctuations in abundance and distribution over the past century due to hunting, bycatches, and exposure to pollutants (e.g., Helle et al., 1976a, 1976b; Helle, 1980; Bergman and Olsson, 1985; Harding and Härkönen, 1999; Bergman, 1999; Bredhult et al., 2008). More recently, climate change has resulted in milder winters in the Baltic, with consequences for sea ice extent and quality and thus breeding habitat (Sundqvist et al., 2012), leading to increased pup mortality (Jüssi et al., 2008). Baltic seals therefore represent ideal species for the development of modelling frameworks to assess the population impacts of multiple stressors.

Phocid seals are capital breeders and have evolved to thrive in highly seasonal environments, including polar environments. A sharp but predictable flux in available energy in the marine food web is driven by spring and autumn peaks in primary production (Stenseth et al., 2004; Stephens et al., 2014). Northern phocid seals also have short lactation periods of 1–3 weeks and a condensed molt when they spend much time on land fasting. They rely heavily on stored energy in their blubber to support life history events with limited food availability. Given the importance of blubber as individual energy reserves and general indicator of ecosystem health, autumn blubber thickness has been adopted as a condition index in seals for the HELCOM monitoring program for assessing the Environmental Status of the Baltic Sea (Kauhala et al., 2017). To this end, decreasing blubber thickness of Baltic seals has been suggested to be linked to reduced availability and quality of primary prey fish species (Hansson et al., 2018; Kauhala et al., 2017, 2018; Kauhala and Kurkilahti, 2020), availability of breeding substrates (Jüssi

et al., 2008) and exposure to xenobiotics (Bergman, 2007), indicating a deterioration of the ecosystem over the past decades.

In order to approach the complex problem of integrating various stressors and evaluate their effects at the population level a common currency is needed. Important also is a framework capable of linking effects across levels of biological organization, including individuals and populations. All stress responses ultimately transfer into an energetic cost for the individual. For example, stress increases metabolism and levels of free radicals which is harmful for the ability to repair DNA, and can increase the cancer risk (Martineau et al., 2002) and autoimmune diseases (Acevedo-Whitehouse and Duffus, 2009). Augmented metabolism also impairs production of antibodies and increases the risk for contracting infectious diseases (Beldomenico et al., 2008). Energetic reserves are also directly correlated to survival and reproduction across animal phyla (Crick et al., 1993; Kleiber, 1961; Nagy et al., 1999), and specifically in gray seals (Kauhala et al., 2019b; Kauhala and Kurkilahti, 2020; Hall et al., 2001, 2002). As such, state-based models are increasingly being used in population biology to account for the condition of individuals, often measured as energy reserves, in the dynamics of populations (McNamara and Houston, 1996; Benton et al., 2006).

Process-based modelling frameworks based on dynamic energy budgets (DEB) are ideally suited to explore how organisms interact with their environment and how they are impacted by multiple stressors. DEB theory in particular provides such a framework as it is well established, has been applied across animal phyla using consistent theory, and is based on first-principles (Kooijman, 2010). DEB theory predicts the flow of energy or mass from the environment to the individual, then allocation to metabolic processes, over the full lifecycle of organisms to determine life-history traits, individual fitness, and ultimately population dynamics (Martin et al., 2013). The Add my Pet inventory, a curated database of DEB parameter values across species, has currently over 2000 species (https://www.bio.vu.nl/thb/deb/deblab/add_my_pet/). DEB models have been published to describe development dynamics in relatively simple and complex organisms, ranging from cyanobacteria (Grossowicz et al., 2017) and copepods (Jager et al., 2016) to mink (*Mustela vison*) (Desforges et al., 2017), elephant seals (*Mirounga leonina*) (Goedegebuure et al., 2018), and right whales (*Eubalaena glacialis*) (Klanjscek et al., 2007). However, because of the complexity of mammals and the lack of empirical data to calibrate such models, DEB theory has been applied more frequently to investigate both developmental and ecological processes in relatively simpler organisms, such as mollusks (Van der Veer et al., 2006; Rosland et al., 2009; Agüera et al., 2017), copepods (Jager et al., 2016) and fish (Einarsson et al., 2011; Nisbet et al., 2012; Stavrakidis-Zachou et al., 2019). Furthermore, few studies explore multiple stressors.

The purpose of this study was to develop a full lifecycle DEB and individual based model (DEB-IBM) for the Baltic gray seal that captured important elements of physiology, life history, and population dynamics. We also aim to showcase potential applications of the calibrated energetic model to predict population responses to select individual stressors known to threaten gray seals and other marine mammals around the world. Specifically, we explore variations of three ecologically important stressors using typified stress scenarios: food limitation, endocrine disrupting chemicals, and infectious disease. We take a phenomenological approach to our stress simulations to simply highlight various approaches to integrate stressors within a DEB-IBM framework. Ultimately, this model framework is intended to provide a guide for future population modelling studies in marine mammals exposed to multiple stressors and contribute to the development of stronger conservation strategies.

2. Material and methods

2.1. Model summary

The model follows individual female gray seals from the Baltic

population as they mature through four life-stages: fetus, nursing, juvenile, and adult. The year, encompassing 365 days, is split evenly into 12 months, and simulations begin on January 1st as day 1, with 100 individuals. The set of ordinary differential equations are solved on a daily time step and no spatially explicit environments are included. All model simulations include a 30 year burn-in period to generate a realistic population age structure and remove the influence of initial conditions. Model output is recorded following the burn-in period over the following 15 years, representing a 5 year expansion phase, a 5 year disturbance phase and a 5 year recovery phase. Details for environmental disturbances are described below.

We follow standard DEB notations and core principles (Kooijman, 2010), with modifications necessary to account for mammalian life history processes as described in Desforges et al. (2019). Individuals are characterized by the four primary state variables used in DEB theory: structure (V), reserves (E), maturity (E_H), and reproduction buffer (E_R). The DEB model defines how energy is taken from the environment and used to fuel the metabolic processes of maintenance, growth, maturation, and reproduction. Food intake is controlled by a scaled functional response (f) that ranges between 0 (no food) to 1 (maximum food intake). Assimilated energy is accumulated in the reserves, where fixed fractions κ and $1-\kappa$ are mobilized and allocated to soma (somatic maintenance and growth) and maturity/reproduction (maturity maintenance, maturation, and reproduction buffer), respectively. After sexual maturation, energy from the reproduction buffer is allocated to the developing offspring during gestation and lactation (Fig. 1). In order to

include the energetic costs of reproduction for adult females, male offspring (50% probability during conception) are removed from the population after the weaning period.

We deviate from standard DEB theory in our dynamics for growth and upregulated assimilation. We implement a prescribed growth model similar to de Roos et al. (2009) in which structural growth follows a predetermined pattern rather than being limited by reserve mobilization (and thus environmental conditions). Prescribed growth, e.g. genetic control on asymptotic size, is exemplified in most aquatic and terrestrial vertebrates (de Roos et al., 2009), and particularly for seals (e.g. Harding et al., 2018). Upregulated assimilation, the additional food intake flux in adult females to cover costly reproductive processes, is modelled as a fixed fraction of the assimilation flux (and thus dependent on food availability; f) and is regulated by the body condition of the animal. Standard DEB approaches for upregulation dynamics could not be followed given that gray seals are capital breeders and thus do not feed concurrently with lactation, thus rely on stored energy (Harding et al., 2007) and cannot increase feeding proportional to pup growth as described in standard DEB Theory. We therefore implement upregulated assimilation as a fixed fraction of regular assimilation, and regulated by energy stored in the reproduction buffer. Full description of the model processes and parameter values are provided in the Supplemental Information (Appendix 1).

The DEB model was incorporated into an individual based model (IBM) to simulate the full life cycle of Baltic gray seals (Fig. 1) and emerging population dynamics. We use average values for lifecycle

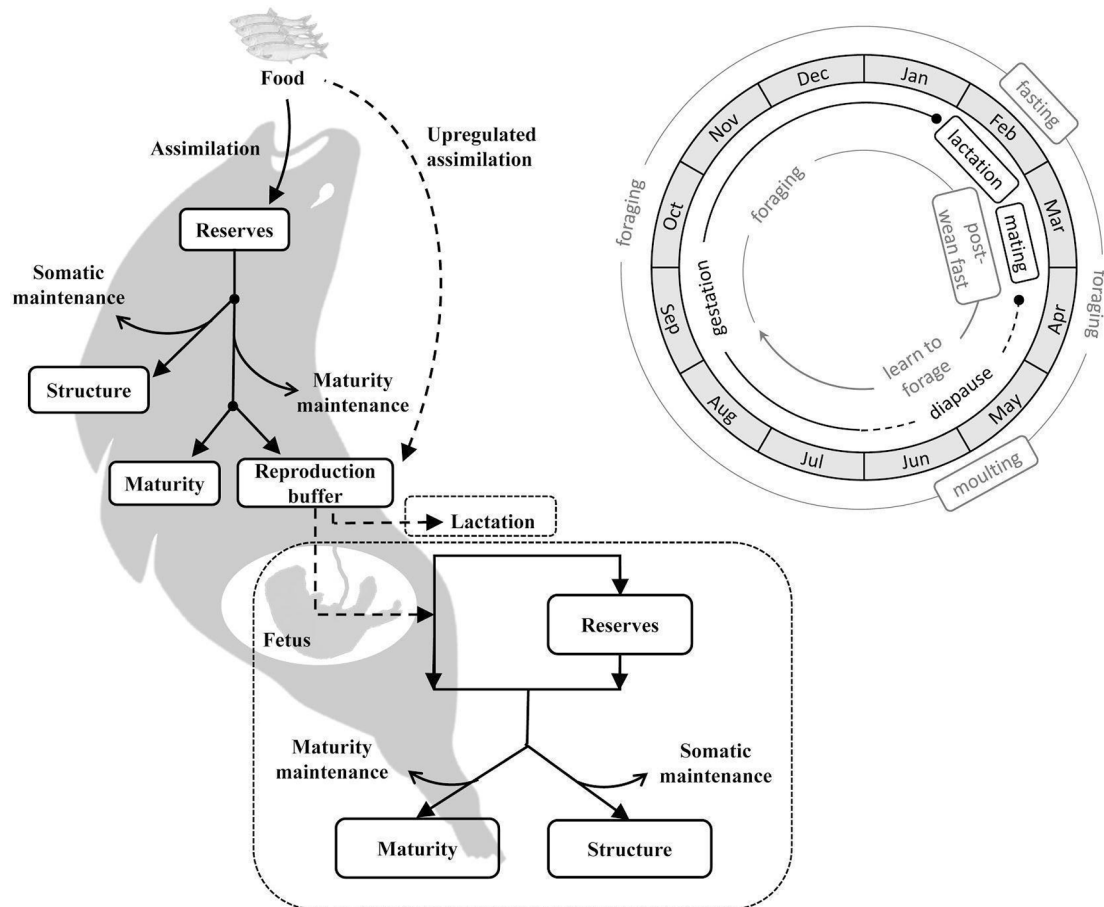


Fig. 1. Schematic flow chart of the bioenergetic model and generalized life history calendar for the Baltic gray seals (*Halichoerus grypus*). Solid boxes in the energy budget schematic indicate the four state variables used to describe the state of an individual at any given time in DEB theory: structure, reserves, maturity, and reproduction buffer. Arrows indicate functions for energy flow that influence the state variables. The circle on the upper right corner describes a calendar year and the timing of the most important life history events in the life of a Baltic female gray seal. The dotted line around diapause indicates the period with no active fetal growth. See Supplementary Information (Appendix 1) for a full description of the variables and model dynamics.

processes (e.g. gestation, lactation period, etc), but acknowledge these can vary considerably. Seals mate in March and gestation lasts approximately 350 days (including a flexible diapause period of approximately 100–120 days). After a two week lactation period in which pups have access to high quality milk, pups are abruptly weaned and endure a post-weaning fast for 28 days, after which they venture to sea to forage for the first time. During this learn-to-forage period, juvenile seals lose body fat and develop lean mass (Hall and McConnell, 2007). There is also a moulting period around May-June during which gray seals remain mostly on land and markedly reduce their food intake (Harding et al., 2007). Stochasticity is built into the model for various processes, namely reproduction (failed implantation, pup abandonment at birth and during lactation), mortality (age-specific background mortality, ageing mortality, condition-related mortality), and individual variability (specific assimilation rate, functional response). Further details on processes implemented in the IBM are provided in Supplemental Information (Appendix 1).

2.2. Population model

The DEB model was implemented as an individual-based model in Netlogo (Wilensky, 1999). Individual state changes happen daily (one time step equals one day) and individuals interact indirectly through different variables, which include stochastic factors that represent the variation in natural populations. We calibrated our modelled population to match observations from Baltic gray seals. Specifically, we aimed to achieve similar population growth rate, life history, and age structure as observed in nature (Harding et al., 2007).

In order to explore the model from a population perspective and obtain predictions about population trends, we created different theoretical scenarios of environmental stressors in order to track model behavior and demonstrate potential model applications. We investigated environmental stress in the form of: reduced food availability ($\varepsilon_{F,t}$), infertility caused by environmental pollutants ($\varepsilon_{P,t}$) and occurrence of infectious diseases ($\varepsilon_{I,t}$). For each type of environmental stress, we created three scenarios and obtained data about individual state changes of different life history traits and summarized them into population variables and structure, with 25 simulations per scenario. We defined a control scenario where none of the environmental stressors mentioned above were present and compared the results with the outcome of the experimental simulations at the population level. We modelled these stressors in isolation and did not consider multiple stress/cumulative impacts.

2.2.1. Environmental stressors: food limitation scenarios

Reduction in food availability ($0 \leq \varepsilon_{F,t} \leq 1$; Figs. S1A–C) was modelled as a reduction in the functional response of an individual. Food availability was assumed to have a proportional effect on the functional response (f) of each individual, such that the effective functional response of an individual was calculated as $\varepsilon_{F,t}f$. When food availability is maximal ($\varepsilon_{F,t} = 1$), the effective functional response is simply f , which is the stage-specific maximum functional response. We compared three food availability scenarios, intended to capture the different types of variation in prey availability, which differed in the dynamics within the experimental interval:

- (A) Strong seasonal flux during one year. Daily food availability was gradually reduced to $\varepsilon_{F,t} = 0.5$ followed by a gradual increase to maximum availability ($\varepsilon_{F,t} = 1.0$) during the first year of the experimental interval (from $\varepsilon_{F,t} = 1.0$ on day 1 to $\varepsilon_{F,t} = 0.5$ on day 182 and back to $\varepsilon_{F,t} = 1.0$ on day 365), followed by maximum availability in subsequent years (Fig. S1A);
- (B) Random prey availability during five years. Food availability levels used in scenario A were scattered within the 5-year experimental interval such that the average food availability

within the experimental interval was identical in scenarios A and B (Fig. S1B);

- (C) Random and low prey availability during five years. A modification of scenario B where the number of days with reduced food availability within the experimental interval was three times the number of days in scenario B and therefore the average food availability level is lower (Fig. S1C).

These scenarios allowed us to assess the effect of food availability when food limitation is distributed over short and long periods of time, and the theoretical energy intake functions also provided a pressure test of the DEB model.

2.2.2. Environmental stressors: pollution scenarios

We also explored the role of a hypothetical environmental pollutant (Figs. S1D–F) with endocrine disrupting properties that reduce female fertility as a function of female conception probability during the breeding season ($P_{P,t}$) as a linear function of pollutant concentration ($C_{P,t}$) in the body of females (mg/kg): $P_{P,t} = \max(0, 1 - 0.005C_{P,t})$. We used this linear relationship between $P_{P,t}$ and $C_{P,t}$ as an approximation of the effect of the pollutant on fecundity. Although there is currently limited data to estimate the intercept and slope of such a relationship, we believe that the values used here fall within a realistic range (Mauritsson et al., 2020). The proposed equation assumes that $P_{P,t} = 1$ when $C_{P,t} = 0$ mg/kg and $P_{P,t} = 0$ when $C_{P,t} = 200$ mg/kg. Because of the lack of empirical data on the bioaccumulation and elimination rates of pollutants, we assumed that the environmental pollutant level (ε_P) represents the daily amount (in mg) of ingested pollutant, the yearly bioaccumulation rate $B_P = 0.2$ represents the daily proportion of ingested pollutant that is incorporated into the chemical composition of an individual and the yearly elimination rate $E_P = 0.1$ represents the daily proportion of pollutant that is eliminated from the body. Because of the lack of empirical data, values assigned to the bioaccumulation and elimination rates are only hypothetical. Because fetuses and nurslings do not forage, the amount of pollutant that is ingested by these life stages depends on the maternal amount $A_{P,t}^M$, the bioaccumulation rate B_P and the elimination rate E_P . Therefore, the pollutant concentration in fetuses and nurslings ($C_{P,t+1}^O$) was calculated as: $C_{P,t+1}^O = [A_{P,t}^O + B_P A_{P,t}^M - E_P A_{P,t}^O] / W_t^O$, where $A_{P,t}^O$ is the total amount of pollutant in the offspring and W_t^O is the mass of the offspring (in kg). With that, the corresponding amount of pollutant transferred to the offspring ($B_P A_{P,t}^M$) is removed from the mother. In juveniles and adults, however, $C_{P,t}$ depends directly on the amount of ingested pollutant and the individual's functional response: $C_{P,t+1} = [A_{P,t} + f B_P \varepsilon_{P,t} - E_P A_{P,t}] / W_t$. We compared the control environmental scenario where $\varepsilon_{P,t} = 0$ mg/day throughout the experimental interval with three scenarios where the daily intake of the pollutant is: (D) $\varepsilon_{P,t} = 7059$ mg/day (Fig. S1D); (E) $\varepsilon_{P,t} = 12707$ mg/day (Fig. S1E); and (F) $\varepsilon_{P,t} = 18355$ mg/day (Fig. S1F). These values were chosen such that a notional adult individual that weighs 100 kg reaches pollutant concentrations of 50 mg/kg, 90 mg/kg and 130 mg/kg, respectively, after 5 years of constant exposure. These concentrations are similar to concentrations of PCBs, a known endocrine disruptor, that have been observed in gray seals in the Baltic Sea.

2.2.3. Environmental stressors: infectious disease scenarios

Finally, we explored the effects of different types of infectious diseases (Figs. S1G–I) on seal population dynamics by incorporating probabilistic functions that regulate infection, transmission and lethality. We assumed that infections can be caused by spillover events (e.g., transmissions from other infected populations or species) and/or by contact between seals within the simulated population. The infection rate caused by spillover ($\varepsilon_{I,t}$) is the yearly probability that any susceptible individual will become infected by external sources of infectious agents. All individuals (with the exception of fetuses) in our model are

susceptible to spillover infection. Additionally, we included a transmission rate (T_I) and a contact rate (C_I) that is proportional to the density of infected individuals in the population. The transmission rate is the probability of transmission of the pathogen among individuals upon contact, and the contact rate is the probability of contact with an infected individual: $C_I = \frac{N_I}{N_T}$, where N_I is the number of infected individuals in the population and N_T is the total population size. Therefore, the probability that a randomly selected individual becomes infected is $P_I = \varepsilon_{I,t} + C_I \cdot T_I$.

We considered an infectious agent that does not affect the developmental dynamics of the infected individuals, but has a lethal outcome with a probability P_D that is positively proportional to the duration of the infection D_I (individuals that have been infected for a longer period of time have a higher probability of death) and negatively proportional to the age of the individual (A) as a consequence of the stronger immune system in adults. Therefore, the probability of death caused by the infection is $P_D = \delta \frac{D_I}{A} \cdot (1 - R_I)$ where δ is the maximum death probability and R_I is the probability of resistance of an individual due to its genetic background. Although included in the model, genetic resistance was not taken into account in the present analysis, where all individuals were assigned $R_I = 0$. We also assumed that infected individuals remain infected for the rest of their lives (chronic disease), which is the case of, for example, herpesviruses and morbilliviruses, which have been reported to cause chronic diseases in seals or other carnivores (Vandevelde and Zurbriggen, 1995; Gulland et al., 1997). We compared three infectious disease scenarios which differed in the environmental dynamics (infection rate caused by spillover events) within the experimental interval as well as the transmission and death rates caused by infections. These were designed to explore the effect of three important components of infectious diseases: rate of infection from external sources, rate of transmission across individuals, and death rate. The three scenarios were:

(G) Infections are non-communicable ($T_I = 0$), occur with an annual infection rate of $\varepsilon_I = 0.2$ during the experimental interval and maximum death probability of $\delta = 0.25$ (Fig. S1G);

(H) Infections are communicable with a yearly transmission rate of $T_I = 0.5$, annual infection rate caused by spillover of $\varepsilon_I = 0.05$ during the experimental interval and maximum death probability of $\delta = 0.25$ (Fig. S1H);

(I) Infections are communicable with a yearly transmission rate of $T_I = 0.5$, annual infection rate caused by external sources of $\varepsilon_I = 0.05$ during the experimental interval and maximum death probability of $\delta = 0.5$ (Fig. S1I).

3. Results

3.1. Model Calibration: Comparison of predicted seal development with empirical data

Our model was calibrated to represent the growth patterns observed in gray seals throughout their life history. Model calibration was based primarily on collected data from databases at the Swedish Museum of Natural History and Finnish Natural Resources Institute (see Kauhala et al., 2017, 2019a, b), where systematic autopsies are performed. Literature data was also surveyed to pull out relevant information on gray seal energetics (see review of data in Appendix 1 Table S4).

Empirical measurements show that body weight increase during fetal development resembles an exponential function and our model simulations capture that pattern well (Fig. 2A). After birth, changes in body weight follow important life history processes and seasonal environmental dynamics. Pups grow rapidly during the short lactation period due to access to energy-rich milk from their mothers. Following lactation, pups are abruptly weaned and lose mass during the post-weaning fasting period, and continue in negative or slight positive energy gain throughout the following year as they learn to forage at sea for the first

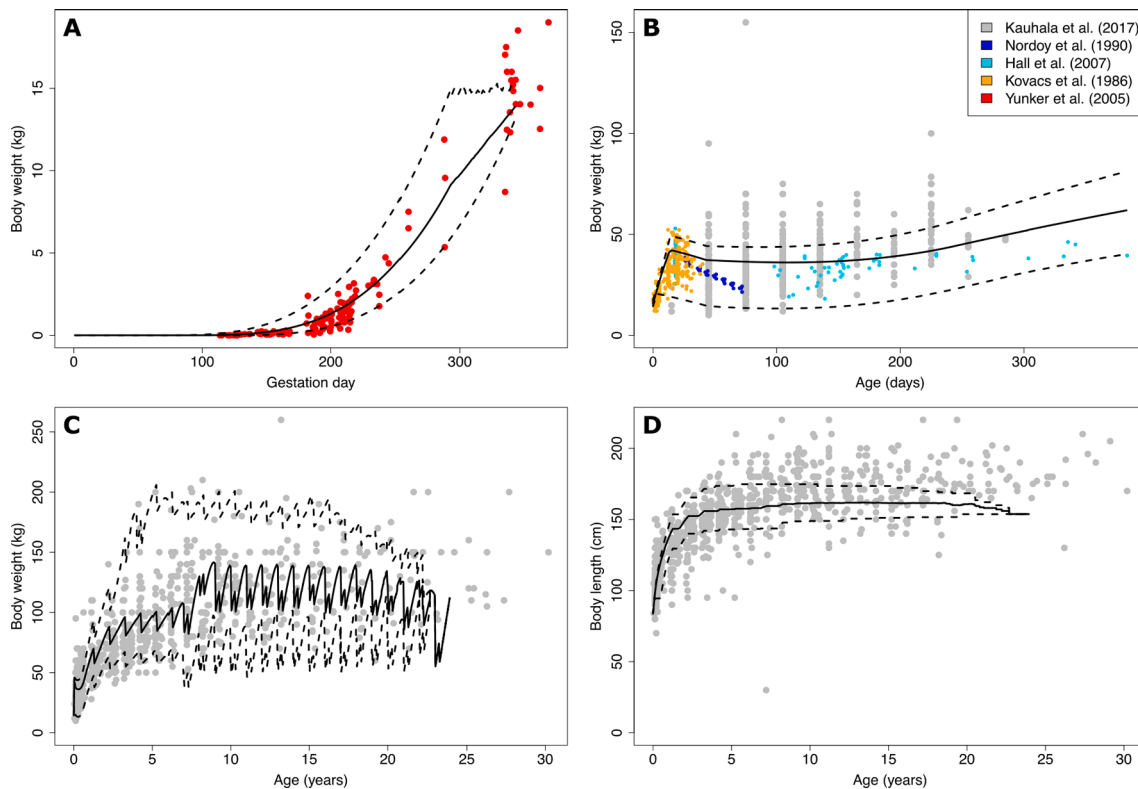


Fig. 2. Simulated growth data from the DEB model vs. empirical observations of gray seal body growth. (A) Body weight during fetal growth. (B) Body weight of weaning pups and juveniles. (C) Lifetime body weight of female gray seals. (D) Lifetime body length of female gray seals. Points represent empirical data, solid lines represent the mean simulated body growth and dashed lines represent the range (min–max) of the simulated data.

time. These dynamics are well predicted by our model simulations assuming variable functional response values during these periods (Fig. 2B). Lastly, asymptotic and seasonal body weight is realistically predicted by the model as a function of reproduction and moulting cycles throughout the year (Fig. 2C). Body length estimates of empirical data are somewhat more scattered and are influenced by sampling error and natural variation from interannual variation in food supply and possibly genetic variation in the population (Fig. 2D).

3.2. Energy dynamics during individual development

We simulate detailed energetics of the gray seal using the calibrated DEB model to show how energy fluxes and storage vary according to the individual life history (Fig. 3, Fig. S2). As with body weight, energy stored in reserves and the reproduction buffer fluctuated throughout the year in adult females as they gained energy from food most of the year, but were in negative energy balance during reproduction and moulting (Fig. 3). Developmental dynamics of energy fluxes show large spikes in most processes (e.g. assimilation, growth, maturity maintenance) at birth, which corresponds to a change in the energy budget from fetus to pup and a sudden increase in energy intake and thus utilization with access to high-quality milk (Fig. S2). Otherwise, metabolic processes follow the same seasonal and life history processes as described above.

To evaluate the temporal developmental dynamics at the population level, we summarized individual information into relevant population metrics (Figs. S3 and S4). As expected, predictions at the population

level stabilized over time and fluctuated according to seasonal life history activities and population age structure. For instance, mean population weight and length decreased as pups were born, and increased thereafter until the next breeding season (Fig. S3).

3.3. Population growth and age structure

Our individual-based model of the gray seal population was calibrated to represent the population in the Baltic Sea (Harding et al., 2007). The model reproduced the observed stable population growth rate of adult Baltic gray seals of seven percent annually ($\lambda = 1.07$). The model also predicted a realistic stable age structure of the population, with younger age classes more abundant and older age classes increasingly less abundant (Fig. 4). We use the results of this calibrated simulation as the baseline for population dynamics in subsequent simulations to assess the effect of different environmental stressors.

3.4. Environmental stressors: food availability

We first assess the influence of various forms of food limitation (change in functional response) on the population, as measured by population size and growth, age structure, and mean weight and age (Fig. 5 and S5). A reduction in food consumption relative to the control population caused a decline in population size due to more frequent deaths by starvation (Scenarios A-C in Fig. 5 and S5) and a decline in the population mean weight throughout the period of food limitation

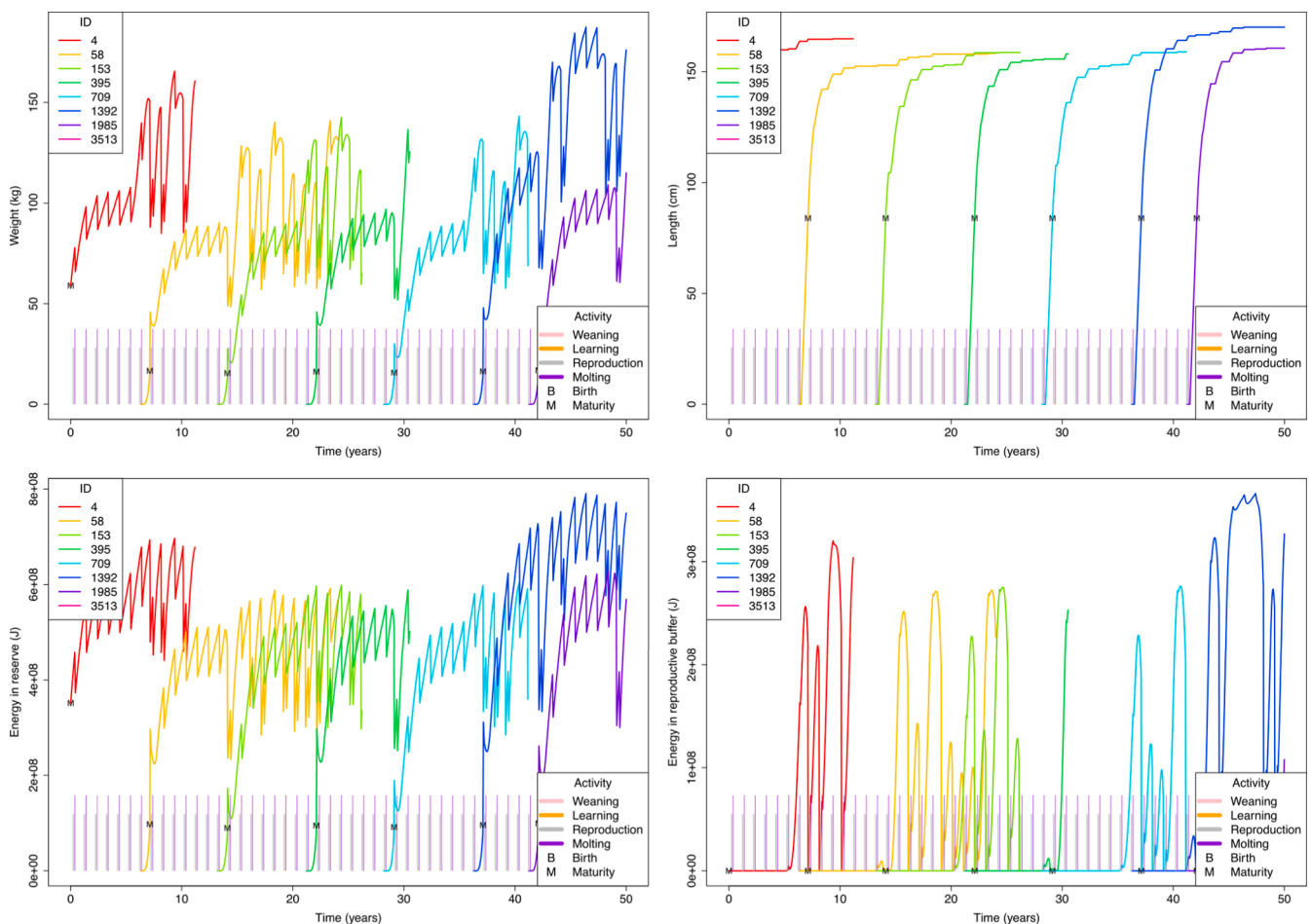
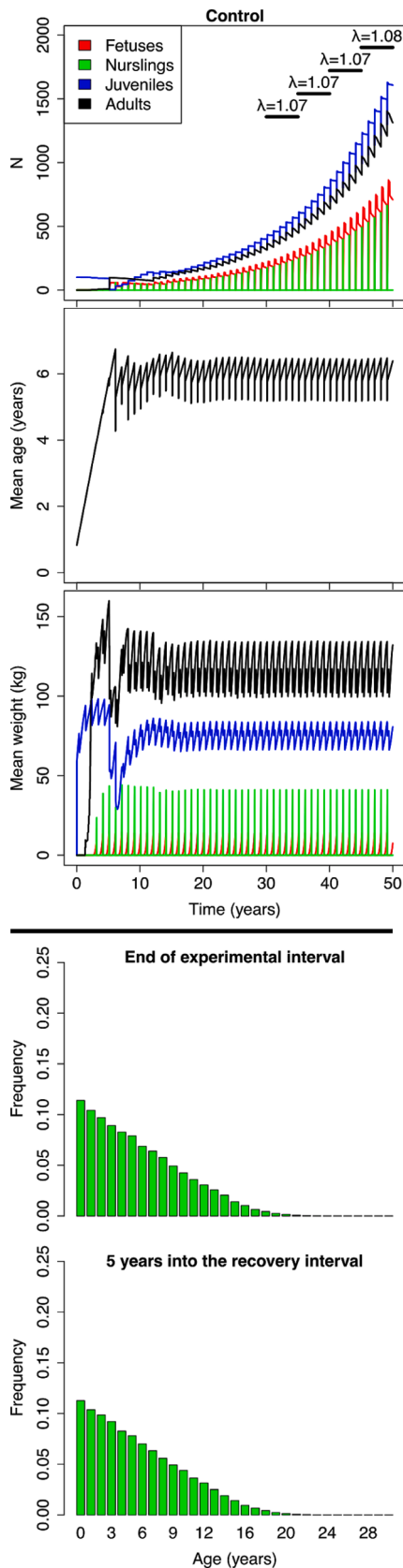


Fig. 3. Dynamics of growth and energy expenditure in eight individual gray seals (ID in the left corner) belonging to a family lineage, as an example of output from the DEB model simulations. Top left: body weight (kg); top right: body length (cm); bottom left: energy in reserves (J); bottom right: energy in reproductive buffer (J). Note that the first individual (ID: 4) belongs to the initial population and all other individuals are her daughters and grand-daughters. Vertical bars indicate the life cycle activities: weaning, learning, reproduction and moulting. Letters indicate birth (B) and time when maturity is reached (M).



(caption on next column)

Fig. 4. Population dynamics resulting from the baseline, control population (without explicit environmental stress). Plots represent average values across all control simulation replicates. Horizontal bars indicate the expansion, experimental and recovery intervals (from left to right) followed by the last five years of the simulation and their respective growth rates (λ). Mean age during the experimental and recovery intervals is ~ 6.1 years. Mean body weight during the experimental and recovery intervals was ~ 48.8 kg. Age distributions at the end of the experimental interval (no environmental stress) and five years into the recovery interval are shown for comparison with the stress-exposed scenarios (Figs. 5–7). Note that the instability in the beginning of the simulations caused by the initial conditions is slowly replaced by a stable pattern.

(Fig. 5; mean body weights of 44.3, 42.6 and 33 kg in scenarios A, B and C, respectively, during the experimental interval). Starved populations became older than non-starving populations due to the higher dependency of the young on sufficient feeding (Fig. 5; mean population age of 6.5, 6.3 and 6.9 years in scenarios A, B and C, respectively, during the experimental interval). The distribution of food limitation events over the 5-year disturbance period was an important factor in predicting population dynamics, affecting λ during the experimental (λ_e) and recovery (λ_r) intervals of the simulations. Food limitation events concentrated within one year (scenario A $\lambda_e = 0.79$ vs baseline $\lambda_e = 1.07$) caused a stronger effect on short-term population dynamics compared to the same and equally stressful events (in terms of total energy reduction) spread over a longer a time interval of five years (scenario B, $\lambda_e = 1.07$). In scenario C, when events of food limitation were relatively more frequent (three times more frequent than scenario A) and the mean food availability was lower, population structure seemed to be only slightly different from scenario A, with a significant reduction in the abundance of younger individuals by the end of the experimental interval. The effect of food limitation was also visible in the mean age of the population, where the lower mean food availability in scenario C led to an increased population mean age (6.8 years) during the recovery interval due to reduced reproduction and increased mortality of the young caused by starvation. The effect of food limitation on mean weight could be observed in all life stages (Fig. S5) including those that did not directly forage from the environment (fetuses and nurslings) because of the indirect maternal effect of lowered energy reserves on fetal and newborn growth and survival. The energetic thresholds chosen for conception and abortion are important in shaping the response at the population level and influence if adult females survive through a period of food limitation or not.

3.5. Environmental stressors: pollution

The second set of environmental stressor simulations examined the population consequences of accumulation of a hypothetical environmental pollutant that specifically targets individual fertility (Fig. 6 and S5). The effect of the pollutant on fertility was based on known concentration thresholds for PCBs in Baltic seals (Roos et al., 2012). The dominant effect of the endocrine disruptor was on the population age distribution. The effect on population mean age depended on tissue pollutant levels and the duration of exposure, with higher levels leading to a greater shift towards an older population mean age. Mean ages during the experimental and recovery intervals were, respectively, 6.1 and 6.2 years (scenario D), 6.2 and 6.4 years (scenario E), and 6.2 and 6.6 years (scenario F). Because of the gradual bioaccumulation of the pollutant over time, the predicted effect of the five-year disturbance period was delayed to the recovery interval and thereafter, when young seals at their peak fecundity had accumulated the pollutant to a level that caused a reduction in fertility for some time after exposure to the pollutant was ceased. There was little to no effect on population mean age due to exposure in older seals because of their already low fertility and short remaining life time. The long-lasting effect (more than five years) of pollutant exposure was also evident on the population growth rate, where λ_r of exposed populations remained lower than that of the

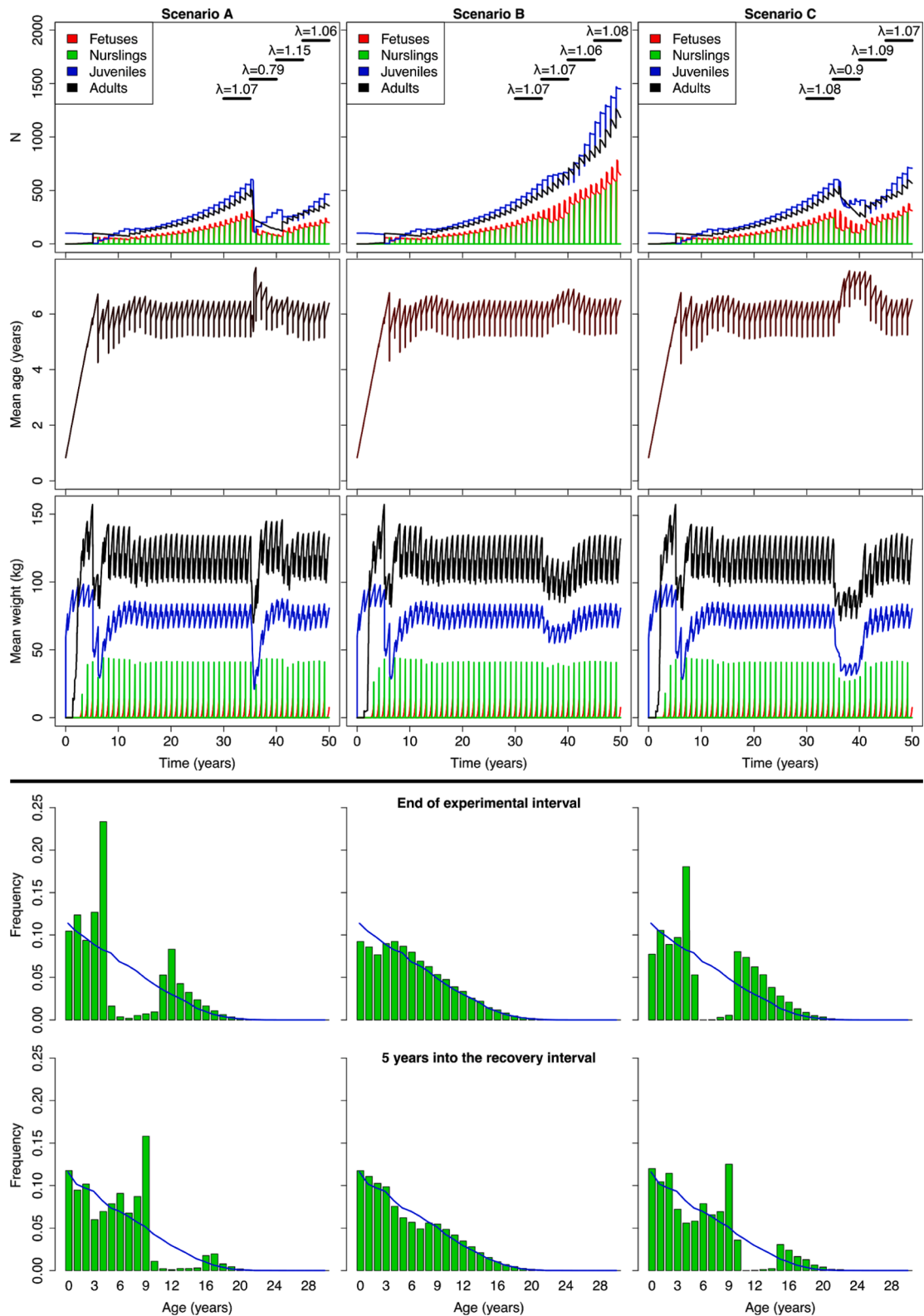


Fig. 5. The gray seal DEB-model was simulated at the population level during a 50 year time interval, recording weakly state changes for all individuals. The simulated population was exposed to three different types of food limitation; a short abrupt decrease in energy (scenario A, left column with graphs), food shortage spread out over five years (scenario B, middle column of graphs) and a three times lower food abundance spread out over five years (scenario C, right column of graphs). The population response was documented in terms of population size (first row), mean age of individuals (second row) and mean weight (third row). Plots represent average values across simulation replicates. Horizontal bars in graphs in the first row indicate the expansion, experimental and recovery intervals (from left to right) followed by the last five years of the simulation and their respective growth rates (λ) are given above each bar. Green histograms represent the population age structure across simulations at the end of the experimental interval (fourth row) and after five years of recovery (fifth row). The blue curves indicate the age distribution of the baseline scenario (control). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

control population, even beyond the recovery interval (Fig. 6). Additionally, because λ is measured in terms of number of adults in the population, changes in λ were minimal (e.g. $<1\%$) during the experimental and recovery intervals. However, it is important to note that potential fertility effects would have likely caused much more delayed effects on λ (beyond the recovery interval) as the reduced younger generation reached adulthood (see age structure in Fig. 6). Furthermore, the increased population mean age caused by pollutant induced infertility led to increased population mean weight due to the increased proportion of older age classes and increased energy reserves from reduced lactational transfer, mean body weights during the experimental and recovery intervals were, respectively, 49.1 and 49.5 kg (scenario D), 49.4 and 50.1 kg (scenario E), and 49.7 and 50.8 kg (scenario F) (Fig. 6).

3.6. Environmental stressors: infectious diseases

The third and final set of environmental stressor scenarios explored the effect of three important components of infectious diseases: rate of infection from external sources, rate of transmission across individuals, and death rate (Fig. 7 and S5). As expected, when the infectious disease was non-communicable (scenario G), the number of infected individuals in the population decreased as soon as the source of infection was eliminated (recovery interval). For a communicable disease (scenarios H-I), the number of infected individuals continued increasing after the original source had been eliminated. With that, a communicable disease with a yearly death rate of 0.25 (scenario H) established itself in the population and reduced the long-term population growth rate during the recovery interval to $\lambda_r = 1.01$ and even lower after the recovery interval ($\lambda = 0.99$). Keeping all else constant, a higher yearly death rate of 0.5 (scenario I) caused a strong reduction in the population growth rate to $\lambda_r = 0.98$ during the recovery interval because of the associated high mortality rate, thus contributing to a rapid decline in the number of infected individuals in the population and possibly extinction in the long-term, if the disease is not eradicated (Fig. 7).

4. Discussion

We developed and calibrated a full lifetime energy budget model for the gray seal, that when coupled to a life history specific individual based model, predicted population dynamics observed in the Baltic Sea. As a showcase of possible model applications, we explored how three important environmental stressors for marine wildlife, namely food limitation, chemical pollution, and infectious diseases, influenced the temporal dynamics of our modelled population. Our modelling framework is process-based, captures the full lifetime and life history events of individuals, and is based on a consistent theoretical description of metabolic physiology, thus adaptable to any species (Kooijman, 2010). Importantly, since metabolic rate (i.e. energetics) is a fundamental biological rate across species (Brown et al., 2004), energy budgets are ideal for modelling the impact of stressors and integrating the effect of multiple stressors on organism physiology, individual fitness, and ultimately population dynamics. We show that stressors leave a unique fingerprint on exposed populations, caused by the interaction of stressor mode of action and population structure. While we do not address the cumulative impact of multiple stressors here, our framework can easily incorporate this, and this is sure to be an important avenue for future experimental and modelling research.

4.1. Dynamic energy budget models

DEB models are being used more and more frequently to simulate developmental dynamics from an energetic perspective. Energy-based traits such as weight are important predictors of health and reproductive success in many species, including gray seals (Kauhala et al., 2019b; Kauhala and Kurkilahti, 2020; Hall et al., 1997, 2007), and our model

describes changes in weight and length throughout the gray seal life cycle. Empirical data shows that during fetal development weight increases exponentially (Yunker et al., 2005) and continues to grow fast after birth during nursing, followed by a period of weight loss during the post-weaning fast (Kovacs and Lavigne, 1986; Nordøy et al., 1990; Hall and McConnell, 2007). In adult seals, seasonal fluctuations in weight are caused by seasonal changes in food availability and fasting during life-history events such as weaning, mating and moulting (Stephens et al., 2014). These dynamics were described in our model in terms of detailed energy storage and allocation.

4.2. Population dynamics and environmental stress

Throughout history, gray seal populations in the Baltic Sea have been exposed to a variety of environmental stressors that have affected population dynamics in different ways. Over the 20th century, the Baltic population declined steeply from more than 80 000 individuals to less than 5 000 (Harding et al., 2007). This decline was caused by a variety of factors that together brought the population to a critical state: extensive hunting (Harding and Härkönen, 1999), pollution by endocrine-disrupting organochlorines (Roos et al., 2012; Nyberg et al., 2015) and infectious diseases (e.g. Duignan et al., 2014; Sonne et al., 2020). Our simulations quantify the impact of these stressors from first principles of energy flux and monitor the result in terms of changes in population traits.

Although levels of different types of stressors are difficult to compare, our study showed that some stressors can cause considerably more harm to the population than others. A reduction in food availability, in particular, caused the most dramatic decrease in the population growth rate and change in population age distribution. However, because of the differences in how each stressor affects the population, it is more reasonable to analyse the effect of each stressor separately. Further studies are needed to implement a multi-stressor modelling approach to assess more realistic population viability.

4.3. Food limitation

With an accurate model of the life cycle dynamics of a species, individual-based simulations become more powerful in projecting population trends under different conditions. Our study showed that food limitation can have negative effects on population growth, and the effect depends on the details of how the environmental variation in prey availability is applied. When the population starves continuously over a period of one year (with up to a 50% reduction in food availability), mortality rates are high and the population can collapse ($\lambda < 1$). However, once prey availability returns to normal, population growth is quickly resumed within five years and can even be higher than in the baseline scenario for a few years (recovery interval) due to age structure effects. Our finding of a stronger effect of food limitation on younger age classes is in line with earlier results from a DEB model of the long-finned pilot whale (*Globicephala melas*), where young lactating females and their calves were shown to be the most affected subgroup in the population under food limitation (Hin et al., 2019). This type of stress has been observed in the past and caused by temporal collapses of prey fish stocks (e.g., Kjellqwist et al., 1995). When prey abundance is lower but fluctuations are spread out over several years (five years), mortality rates are similarly high but the average growth rate years after prey abundance has returned to normal (recovery interval of five years) is significantly increased due to effects on age distribution before it returns to the baseline growth rate. This effect caused by disturbances in the age distribution is important for conservation because in models of population viability (PVA) population growth rates are assumed to return to their full capacities as soon as density dependence is relieved. Thus, future work should investigate how this time lag can affect population extinction risk of species affected by periods of food limitation. Overfishing is one of the main potential causes of food limitation to seals in

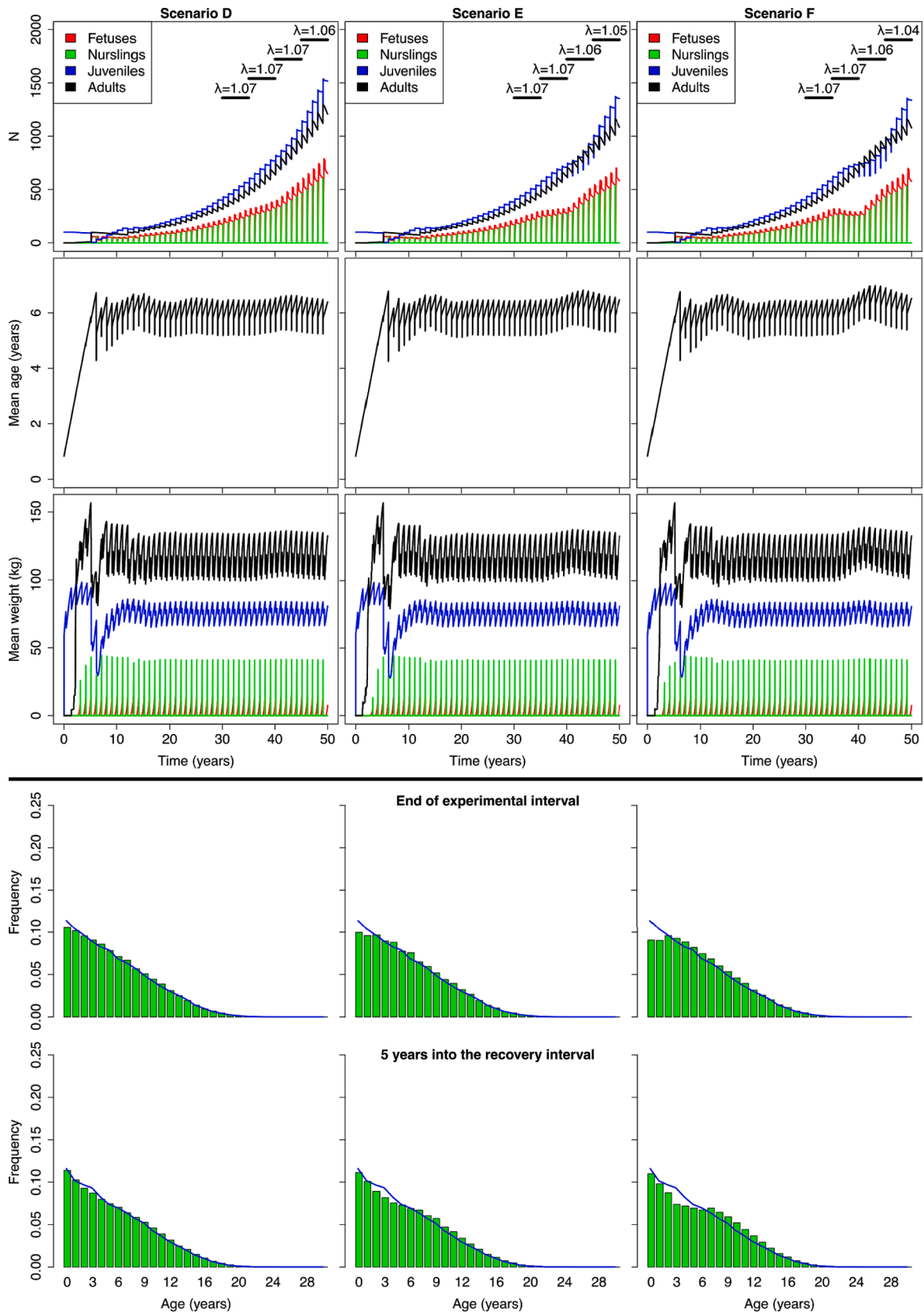


Fig. 6. Population response to reduced fecundity caused by an endocrine disrupting pollutant (scenarios D-F) in terms of population size (first row), mean age of individuals (second row) and mean weight (third row). Plots represent average values across simulation replicates. Horizontal bars indicate the expansion, experimental and recovery intervals (from left to right) followed by the last five years of the simulation and their respective growth rates (λ). Green histograms represent the average population age structure across simulations at the end of the experimental interval (fourth row) and after five years of recovery (fifth row). The blue curves on age distributions indicate the age distribution of the baseline scenario (control). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

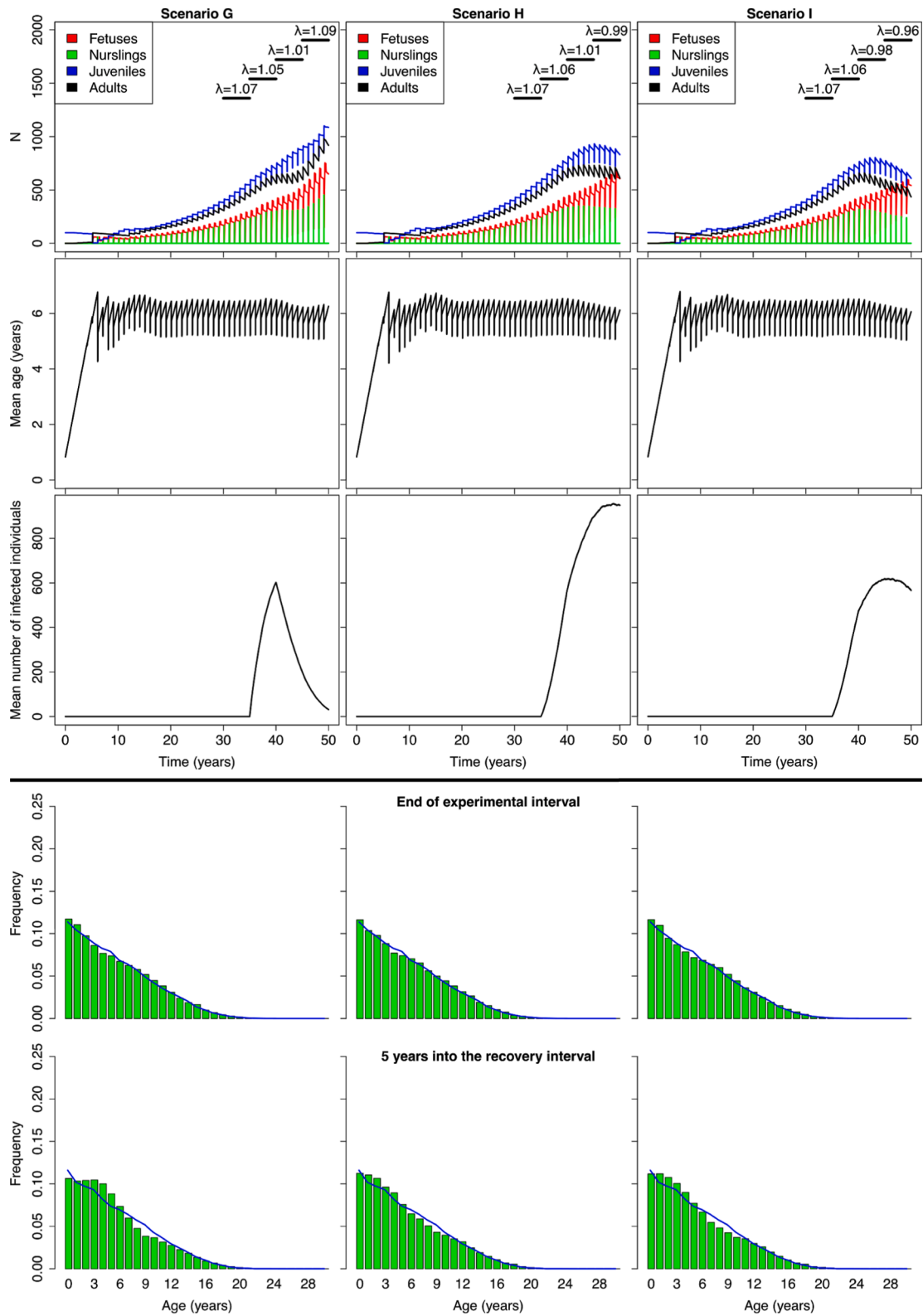


Fig. 7. Population response to infectious diseases (scenarios G-I) in terms of population size (first row), mean age of individuals (second row) and mean weight (third row). Plots represent average values across simulation replicates. Horizontal bars indicate the expansion, experimental and recovery intervals (from left to right) followed by the last five years of the simulation and their respective growth rates (λ). Mean ages during the experimental and recovery intervals were, respectively, 6.1 and 6.0 years (scenario G), 6.1 and 6.0 years (scenario H), and 6.1 and 6.0 years (scenario I). Green histograms represent the average population age structure across simulations at the end of the experimental interval (fourth row) and after five years of recovery (fifth row). The blue curves on age distributions indicate the age distribution of the baseline scenario (control). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

the Baltic region. The fishery catch is mostly composed of herring, sprat and cod, which also happens to be the most important prey species of gray seals (Hansson et al., 2018). Another source of food limitation is the interspecific competition between seals and other animals (Bogstad et al., 2015) or even between different species of seals (Hansson et al., 2018; Kauhala and Kurkilahti, 2020), which can further increase the negative impact of fishery. The recently observed declining trend in population numbers in the Baltic may be related to the effect of reduced energy intake on maternal condition and fecundity (Kauhala et al., 2017, 2019b; Kauhala and Kurkilahti, 2020), a situation that is likely applicable to many stressed marine mammal populations.

4.4. Pollutants

Another source of stress for the population of gray seals is pollution by endocrine-disrupting chemicals (e.g., PCBs), which have been found in tissues of Baltic species, including seals and the fish they consume (Elmgren et al., 2015; Nyberg et al., 2015). Studies have shown that PCB accumulation in tissues through consumption of contaminated fish might be the underlying cause of the historical disruption of the reproductive system and documented sterility of seals (Helle et al., 1976a, 1976b; Bergman, 1999; Roos et al., 2012). These observations inspired our pollutant section of the model, although our model does not claim to mirror exact PCB effects and dynamics. Furthermore, the effects of pollutants go beyond the reduction in fertility. Many pollutants (persistent organic pollutants in particular) can affect lipid metabolic rates in, e.g., seals (Robinson et al., 2018) and polar bears (Routti et al., 2019). Although these effects were not explored in our model, they certainly affect energy reserves and should be explored in future studies using a DEB approach.

Increased pollutant concentrations in lower trophic levels have a proportional effect on pollutant concentrations in top predators (e.g., seals) through bioaccumulation and biomagnification processes (Nyman et al., 2002). Furthermore, pollutants such as PCBs can be transferred from mother to pup during pregnancy and lactation (Debiec et al., 2003), which means that the effects of PCBs can be observed years after PCBs levels have decreased in the ecosystems. We show that higher environmental pollutant levels lead to a higher population mean age and smaller population size, which is a result of the lower pregnancy rate and natural mortality in the older generations. Furthermore, the effects on population growth rate were delayed, and our experimental population showed a decline in population growth rate years after exposure to the pollutant. It is important to note that we model only one chemical threat, but in reality wildlife populations are exposed to hundreds of compounds simultaneously which may act via similar modes of action or on different physiological endpoints (e.g. Letcher et al., 2010). While it was outside the scope of this study, it is important to consider cumulative impacts from multiple pollutants for wildlife risk assessment. Nonetheless, the reduced growth rate modelled here in a relatively short-term exposure window, highlights the importance of taking the effects of pollutants into consideration in the design of management plans for seals and in estimating sustainable levels of hunting quotas. It is very easy to overexploit slow growing marine mammal populations as history has proven (Lotze et al., 2017).

4.5. Infectious diseases

Environmental stress can also come in the form of infectious diseases. Baltic populations of gray seals have experienced several waves of infections caused by different pathogens during the last decades (Sonne et al., 2020). Common parasites include acanthocephalans (Lakemeyer et al., 2020), trematodes (Neimanis et al., 2016), nematodes (Leidenberger et al., 2007; Zuo et al., 2017) and viruses (Dietz et al., 1989a, 1989b; Heide-Jørgensen et al., 1992; Härkönen et al., 2006; Duignan et al., 2014). Although many of these parasites do not have major consequences for population growth, occasional outbreaks have contributed

to population decline over time and can affect immunogenetics and long-term population viability (Näpflin et al., 2019). For example, epidemics of the phocine distemper virus (PDV) caused mass mortality in harbor seals in 1988 and 2002 in the adjacent Kattegat, Skagerrak and North Sea (Dietz et al., 1989a, 1989b; Heide-Jørgensen et al., 1992; Härkönen et al., 2006, 2007; Duignan et al., 2014). Many pathogens can cause a wide range of serious symptoms, induce abortions, reduced fitness, and are transmitted between individuals, magnifying its effect in the population (Sonne et al., 2020). Because of their severity for several species of pinnipeds, morbilliviruses such as canine distemper virus (CDV) (Kennedy et al., 2000; Osterhaus et al., 1988) and PDV have been major causes of concern for seal conservation. Our model shows how communicable diseases can significantly increase the impact of a pathogen in a population, even when spillover infection rates are relatively low. While our study did not reflect any specific infectious disease, we provide a basic framework from which future studies may explore select host-pathogen dynamics of interest, given appropriate parameterization. In our model, we show outcomes that are already known from epidemiological studies, but it is important to stress that diseases can substantially affect population growth rate and age distribution. Future studies must address the relationship between infectious diseases (or diseases in general) and specific changes in energy dynamics so that our model can be tailored to address energetic costs and developmental changes associated with such diseases.

4.6. Model challenges and future direction

Our process-based model of gray seal metabolic physiology reproduced observed patterns of Baltic seal growth and population dynamics, and predicted potential population impacts from hypothetical stressors. To capture realistic dynamics of survival, reproduction, and growth at different food levels, it was necessary to implement a prescribed growth model and year-round upregulated assimilation dynamics for mature females, both non-standard approaches in DEB Theory. Our assumption of prescribed growth, while novel for DEB models, is well accepted in the literature for most large vertebrates (Sebens, 1987), including seals (Harding et al., 2018). The dynamics for upregulated assimilation are more difficult to define due to lack of detailed information on feeding rates in reproductive and non-reproductive females throughout the year. Reproductively active gray seals in captivity are reported to consume greater annual quantities of food than non-reproductive females (Kastelein et al., 1990), but the mechanisms underlying the seasonal intake rates are less understood. We considered the simplest approach possible and calibrated parameters through model testing and pattern-oriented modelling, but acknowledge that further work is needed to better define these processes, especially in capital breeders where standard DEB approaches cannot be applied because of the temporal disconnect between offspring growth and maternal feeding.

Our model is not spatially explicit and does not account for surface area related maintenance costs associated with thermoregulation (only in a simplistic manner by the minimum threshold in energy levels required for survival). We acknowledge that these are important aspects of gray seal ecology and seasonal energetics, but to incorporate these requires considerable work to integrate aspects of animal behavior and memory, prey distribution and quality, spatio-temporal environmental data, and information on the physiological response to ambient temperature, among others. These all require considerable effort, and will surely be the focus of future DEB-IBM applications in different species. While our food limitation simulations integrated stressor impacts into the energy budget model, the pollutant and disease scenarios were not directly modelled via impacts on energetics (e.g. targeted non-energy related fertility and survival). Our purpose here was to simply showcase simple stress simulations and population dynamics, and thus we did not strive to develop complex and realistic stress models. However, for more realistic and mechanistic models, this is a critical component to capture energy-driven stress impacts on individuals and populations,

such as transient and life stage specific effects (e.g. Ashauer et al., 2016; Goedegebuure et al., 2018), physiological trade-offs (e.g. Desforges et al., 2018), complex endocrine disruption (e.g. Murphy et al., 2018), ecosystem interactions and extrapolating across biological scales (e.g. Fan et al., 2020; Murphy et al., 2018), and impacts from multiple stressors (e.g. Gergs et al., 2013).

5. Conclusion

We construct a detailed dynamic energy budget model for the gray seal, and illustrate how to generate quantitative predictions about the effects of different individual environmental stressors on both developmental and population traits. Our modelling framework is based on a mechanistic underpinning of metabolic physiology, which is broadly applicable across animal phyla. Although we illustrate simple stress scenarios, future applications of the model can target specific stressors (e.g., new emerging pollutants) and develop submodels connected to our general framework including metabolic and health costs. Thus, our model can be used to test the expected long-term effects from new substances on population dynamics *in silico*, before they happen, providing predictions that can guide conservation efforts. Importantly, novel model applications require calibration and validation with species data on metabolic costs for various physiological processes as well as stress-related effects on energetics and associated life history traits. Of great interest for future research is to integrate sub-organismal impacts of stressors (e.g. cellular and molecular changes) into the mechanistic energy budgets framework that would facilitate the investigation into the cumulative effects of multiple stressors across the full lifecycle of the organism. This framework can be invaluable for the development of management strategies in the Baltic Sea and other highly stressed environments.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Author contributions

WTAFS, JPD and GM conceived the numerical model, wrote the script and ran the simulations. KCH, WTAFS and JPD outlined the conceptual framework and defined the research questions. All authors contributed to the implementation of the research, the discussion of the results and the writing of the manuscript.

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.envint.2020.106145>.

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