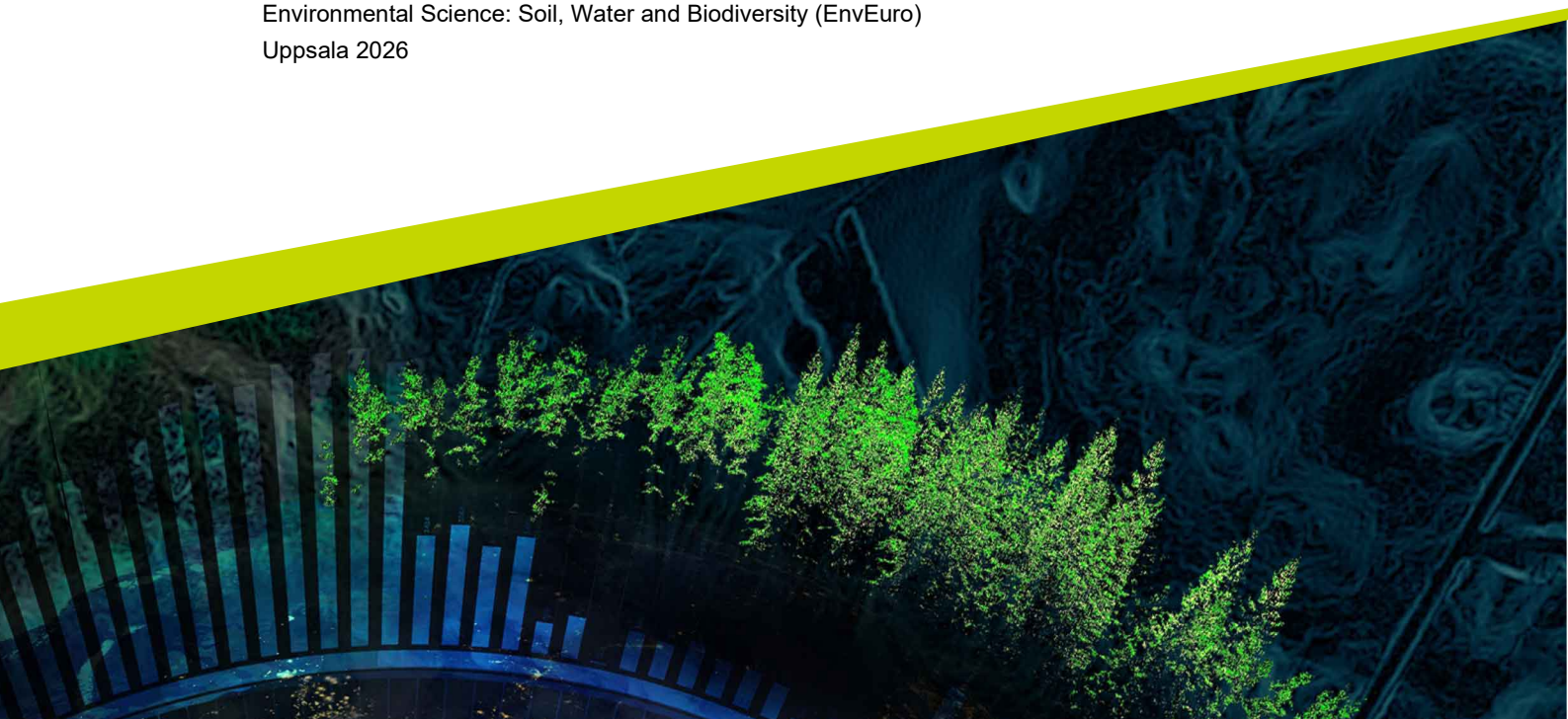
How does warming affect population dynamics of herring and cod in a seasonal environment?

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Abstract

Warming changes population dynamics of interacting fish species, from these, predator-prey interactions are one of the most important because they change the dynamics of food chains. Warming can alter dynamics of predator-prey populations by affecting individual physiology, such as metabolism, as well as consumption rates, leading to changes in growth, reproduction and mortality. Population dynamics of interacting predator-prey species have mostly been studied using non-seasonal models, and therefore little is known about how warming affects fish population dynamics in seasonal environments. Including seasonality in certain regions likely matters as resource availability and temperature fluctuate there throughout the year, influencing feeding, growth, and species persistence under warming. This study investigates how warming affects the population dynamics of interacting cod and herring using a dynamic population model, which includes seasonality. The model accounts for how cod and herring dynamics emerge from their temperature-dependent fish physiology, feeding, and prey dynamics. The results show that biomass levels increase with warming, whereafter the populations suddenly go extinct. Seasonality may influence the mechanisms leading to extinction, through its influence on the energetic mismatch between food intake and metabolism. Warming can alter apart from biomass levels also population cycles' periodicity and amplitude. With warming the results show that population cycles might become more extreme. Furthermore, interactions between predator (cod) and prey (herring) alter how warming affects population dynamics. These results highlight the importance of taking both seasonality and species interactions into account when studying the effect of global warming on population dynamics.

Keywords: Global warming, climate change, predator-prey, seasonality, community dynamics, food webs

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Abbreviations

Abbreviation	Description
SLU	Swedish University of Agricultural Sciences
DOY	Day Of Year
Eq.	Equation
Fig.	Figure
g	gram
Mg O_2/h	milligrams oxygen per hour

1. Introduction

Global warming changes population dynamics across ecosystems (Lindmark et al. 2017). Understanding the mechanisms underlying these changing population dynamics requires insight into how temperature influences species' physiology, as well as species interactions. An individual's metabolism and consumption rates depend on temperature and body size (Lindmark et al. 2022). Lindmark et al. (2022) found that metabolism increases more rapidly with body mass than consumption. The influence of temperature on consumption rate is unimodal, while metabolism increases exponentially with temperature (Lindmark et al. 2022). Due to the influence of temperature on size-dependent metabolism and consumption rate, an increase in temperature can lead to faster body growth, earlier maturation and increased mortality (Huss et al. 2019; Niu et al. 2023; Tye et al. 2022). These warming-driven processes contribute to shifts in species distributions, to deeper waters and towards the poles (Perry et al. 2005; Sorte et al 2010). Moreover, they influence how sensitive species are to temperature and can therefore, for example, make some species outcompete less temperature-tolerant species (Kordas et al. 2011). Extinction of species and shifts in species distribution therefore lead to changes in fish community compositions (Kordas et al. 2011).

Another consequence of the size-dependent acceleration in metabolism and consumption rates with temperature is that smaller individuals have a higher optimal growth temperature than larger individuals, which with sufficient resources available leads to an increase in body growth of younger individuals but less so in older and larger ones (Lindmark et al. 2022). This in turn can cause a shift in population composition towards smaller, younger, and energetically more efficient individuals (van Dorst et al. 2019). Furthermore, higher temperatures can lead to earlier maturation at a smaller size (Niu et al. 2023). This may influence population growth rates negatively as larger females contribute far more to population replenishment than many smaller females of the same total biomass (Barneche et al. 2018). Interactions among species often depend on their body size therefore, changes in size distribution due to warming influence species interactions (Lindmark et al. 2019).

A common and important example of species interactions in a diverse array of communities is intraguild predation. Intraguild predation is defined as predation that happens among potential competitors. It occurs when a predator and its prey share at least one prey resource (Polis et al. 1989). In intraguild predation systems there can be a positive feedback where predators inhibit the prey's competitive impact on juvenile predators by feeding on them, so that predator and prey can coexist, a mechanism called 'cultivation' (Walters & Kitchell 2001). In such systems, warming will enforce the competition between juvenile predators and

prey, because the predation on prey is weakened as adult predators are hit hardest by warming due to their large body size. This leads to a decline in predators, resulting in the loss of a predators' cultivation mechanism (Thunell et al. 2021). As a consequence, there is instead depensation, that is a negative feedback. This happens when there are too few adult predators to reduce interspecific competition, which therefore hampers the juvenile predator development and growth, and thus population growth will be constrained (Walters & Kitchell 2001). Ultimately, collapse of predator populations may occur when there is a loss of cultivation mechanism due to warming (Thunell et al. 2021).

Other modelling studies also predict that warming shifts dynamics of predator and their prey (Lindmark et al. 2019; Fussmann et al. 2014). Lindmark et al. (2019) investigated the effects of warming on predator-prey dynamics using a dynamics stage-structured biomass model. They found that depending on which consumer life stage predators feed on, predator biomass densities declined with warming gradually or through collapses. This vulnerability of predators to warming is further supported by Fussmann et al. (2014), who showed with a bioenergetic model that while warming initially stabilised population oscillations, predator extinction through starvation followed once a critical temperature threshold was exceeded. These studies, along with others (Ohlberger et al. 2011; Bentley et al. 2017; Kuo et al. 2022), do not incorporate seasonality, however seasonality might be important for understanding how warming affects predator-prey dynamics in real systems. Biological processes in marine environments are inherently periodic and discontinuous, rather than continuous. Ignoring seasonality can therefore lead to unreliable or biased estimates of population dynamics and community structure (Xia et al. 2021). Croll et al. (submitted) incorporated seasonality when studying the effects of heat waves using a size-structured model of herring feeding on two prey types. However, their study did not include a predator of herring. Consequently, the effects of warming on predator-prey dynamics including seasonality remain unclear.

This study aims to address the following question: How does warming affect population dynamics of herring and cod in a seasonal environment? Specifically, the analysis will focus on how warming changes biomass levels, population cycles, and the conditions under which populations can persist. I study this using cod and herring in the Baltic Sea as a case study, as the Baltic Sea is a relatively simple and climate-sensitive ecosystem in which cod and herring occupy ecologically important roles within the food web (Ojaveer et al. 2010; Reusch et al. 2018). To analyse the effects of warming on dynamics of interacting cod and herring I use a dynamic population model. The model includes a seasonal environment in which dynamics of the cod and herring populations arise from their respective temperature-dependent fish physiology and feeding, and temperature dependent dynamics of their invertebrate prey.

2. Methods

2.1 Overview of the model

To study the effects of warming on the dynamics of interacting cod and herring, I use a dynamic population model based on the physiologically structured herring model of Croll et al. (submitted). This model accounts for seasonal variation in light and temperature. It also accounts for temperature-dependence of invertebrate prey (as well as light-dependence of zooplankton), of survival of herring eggs and larvae, and physiological and ecological processes of juvenile and adult herring. During the reproduction period, eggs are released once every three days following a hump-shaped distribution. Herring individuals born on the same date are grouped into a cohort. Individuals within the same cohort have the same physiological characteristics, such as biomass, length, condition, etc. Herring feeding activity and consumption efficiency depend on body size, as well as temperature, with individuals undergoing an ontogenetic shift as they grow from feeding predominantly on zooplankton to also including small benthic invertebrates, hereafter referred to as 'small benthos'. These resource communities are temperature- and light dependent. For example, zooplankton is very reliant on the light-dependent productivity of phytoplankton, therefore it is assumed that zooplankton productivity decreases during winter due to low light availability. Assimilated energy is used to cover maintenance costs of herring, and the remaining energy is invested in growth. The effect of temperature on the metabolic rate of herring depends on body size. The energy for growth is allocated to structural and reversible mass. The body condition of herring is the ratio of reversible mass to structural mass, and it determines how much energy can be allocated to reproduction. Maturation happens when herring reaches 14 cm, after which the herring can reproduce. At the start of the reproduction period, all adult individuals convert part of their reversible mass to eggs, while retaining a minimum body condition. Eggs and larvae experience temperature-dependent mortality, while juveniles and adults are subject to background-, size specific-, fisheries- and starvation mortality that are only indirectly dependent on temperature, via feeding, maintenance and their resources (Croll et al. Submitted).

To this model I have added cod, a predator on herring. The cod is stage structured and divided into five stages: small juveniles, large juveniles, small adults, large adults, largest adults. Cod also feeds on zooplankton and small benthos and thereby competes with herring for these preys. In addition, they feed exclusively on large benthic invertebrates (i.e., *Saduria entomon*), hereafter referred to as 'large benthos' and on herring. Moreover, cod predate on their own juveniles, resulting in cannibalism. They shift between these prey types, as they also exhibit an ontogenetic shift based on their body size. Seasonality is also

incorporated in the cod dynamics. Cod has a reproduction period during which they continuously release eggs following a hump-shaped distribution. Furthermore, cod dynamics are also temperature dependent through its temperature-dependent processes such as egg survival, handling time and attack rate on their preys, as well as maintenance energy and transition rates between life stages. This links warming directly to individual growth and predator-prey interactions.

To investigate how population dynamics change with increasing temperatures, I did a bifurcation analysis over temperature. To make sure that the studied dynamics are in equilibrium, for each temperature I let the model run for 100 years, thereafter, I studied the last 10 years of those 100 years. Based on the observed shifts in dynamics shown in the bifurcation graphs, I selected different temperatures for which I illustrated the dynamics (time series) of different variables to investigate how warming alters the population dynamics of cod and herring, and to understand the mechanisms behind it. To better understand how warming influences the interactions between cod and herring, I compared the effects of warming on the dynamics of herring without cod with the effects on its dynamics when both species were included in the model, and vice versa. For the time series graphs, the start of a year is equal to the start of the herring reproductive season, which in the model is set to 5th of May.

2.2 Formulas

2.2.1 Length-classes of cod

The cod in this model is stage structured. The population is divided into five stages depending on body size, prey preference and maturation status (Table 1). The index '*j*' represents the index of the cod stage. Apart from these five stages, there is C0, representing the egg buffer containing the biomass allocated to reproduction for individuals that are not born yet.

Table 1: Description different cod stages and the resources they consume.

Cod stage (j)	Description
1	Small juveniles feeding on zooplankton and small benthos
2	Large juveniles feeding on small and large benthos, and herring
3	Small adult feeding on small and large benthos and herring
4	Large adult feeding on small and large benthos and herring
5	Largest adults feeding on small and large benthos and herring

Table 2 contains the length limits, representative length and weight of each cod stage. Equation 1 calculates the representative weight based on m_{min} and m_{max} representing the initial (i.e. minimum and maximum size limit) size (standard weight) of a certain stage. The length scales allometrically with the weight (Eq. 2).

Table 2: The length limits, representative length and -weight for each cod stage.

Cod stage	1	2	3	4	5
Length range (cm)	0,39-15	15-30	30-55	55-100	100
Representative length (cm)	7	22	42	77	100
Representative weight (g)	3	119	822	5074	10986

Calculation of representative weight and length:

$$w = \frac{m_{max} - m_{min}}{\ln(m_{max}) - \ln(m_{min})} \quad (1)$$

$$l = \lambda_{1c} * w^{\lambda_{2c}} \quad (2)$$

Temperature (T) is implemented in different functions through the Arrhenius function (ΦArr) which shows an exponential increase with temperature, and Sharpe Schoolfield function (ΦSS), which shows a hump-shaped relationship with temperature.

$$\Phi_{Arr}(T, E_A) = \exp\left(-\frac{E_A}{k_B}\left(\frac{1}{T} - \frac{1}{T_r}\right)\right) \quad (3)$$

$$\Phi_{SS}(T, E_A, E_D, T_H) = \frac{\exp\left(-\frac{E_A}{k_B}\left[\frac{1}{T} - \frac{1}{T_r}\right]\right)}{1 + \exp\left(-\frac{E_D}{k_B}\left[\frac{1}{T} - \frac{1}{T_H}\right]\right)} \quad (4)$$

2.2.2 Cod biomass dynamics

Cod biomass dynamics are described for the different cod stages (Eq. 5-10), where C_j is the biomass of cod in stage j, γ_j is the stage transition, v_j is the biomass production, k_j is the fraction of net biomass production that individuals invest into somatic growth, and μ_j represents the mortality. Some terms have a superscript '+', which indicates that they are restricted to non-negative values and equal to zero when negative values would occur. The term F_c represents the release rate of the egg buffer into the first cod stage.

$$\frac{dC_0}{dt} = (1 - k_3)\, v_3{}^+(T)C_3 \; + (1 - k_4)v_4{}^+(T)C_4 \; + v_5{}^+(T)C_5 - F_c C_0 \quad (5)$$

$$\frac{dC_1}{dt} = \; F_c C_0 + v_1(T)C_1 \; - \; \gamma_1{}^+(T)C_1 \; - \; \mu_1(T)C_1 \quad (6)$$

$$\frac{dC_2}{dt} = \gamma_1{}^+(T)C_1 \; + \; v_2(T)C_2 \; - \; \gamma_2{}^+(T)C_2 \; - \; \mu_2(T)C_2 \quad (7)$$

$$\frac{dC_3}{dt} = \gamma_2{}^+(T)C_2 + v_3(T)C_3 - (1-k_3)\,v_3{}^+(T)C_3 - \gamma_3{}^+(T)C_3 - \mu_3(T)C_3 \quad (8)$$

$$\frac{dC_4}{dt} = \gamma_3{}^+(T)C_3 + v_4(T)C_4 - (1-k_4)\,v_4{}^+(T)C_4 - \gamma_4{}^+(T)C_4 - \mu_4(T)C_4 \quad (9)$$

$$\frac{dC_5}{dt} = \gamma_4{}^+(T)C_4 + v_5(T)C_5 - v_5{}^+(T)C_5 - \mu_5(T)C_5 \quad (10)$$

2.2.3 Growth of cod

The net biomass production (v_j) is the product of the assimilation efficiency of cod (k_{ec}) and the ingestion rate of cod (I_j) minus the maintenance energy of the cod (E_j). The difference in net biomass production for the different stages is due to the stage-specific difference in diets and their size- and temperature-dependent parameter values.

$$v_j(T) = k_{ec}I_j(T) - E_j(T) \quad (11)$$

The maintenance energy scales allometrically with representative weight ($\overline{w_j}$). It is temperature dependent and follows an Arrhenius function in which the activation energy depends on the representative weight.

$$E_j(T) = \Phi_{Arr}\left(T, E_{AMC} + E_{iMC}ln\left(\overline{w_j}\right)\right)\rho_{1c}\overline{w_j}^{\rho_{2c}} \quad (12)$$

Transition to a particular life stage is described by Equation 13. In the equation, the product k_jv_j represents the weight-specific somatic growth rate, μ_j represents the death rate, and z_j is the ratio of the initial and final body size of a particular life stage, it reflects the size range through which an individual must grow to transition to the next stage. Weight-specific transition rate at population level is consistent with the individual level when assuming that individuals in a particular life stage grow in body size at a weight-specific rate, while experiencing throughout their entire stage a per capita death rate. In this model, the transition rate indirectly depends on temperature, as biomass production depends on temperature via the temperature-dependent rates of feeding and maintenance, as well as of resource dynamics.

$$\gamma_j(T) = \frac{k_jv_j(T) - \mu_j}{1 - z_j{}^{1-\mu_j/\left(k_jv_j(T)\right)}} \quad (13)$$

2.2.4 Cod reproduction

The energy that is allocated for reproduction during the year will be stored as eggs in an egg buffer of surviving eggs. These eggs are then released during the reproduction period following a hump-shaped continuous distribution (Fc). ζ_c represents the reproduction biomass release rate for cod, which determines the steepness of the hump-shaped distribution. The start of the reproduction period occurs on the same day each year (t_c), and it will continue for a fixed duration

(Δ_c). Egg survival is determined by temperature and the maximum egg survival (R). The term F_c represents the release rate of the egg buffer into the first cod stage.

$$F_c = \begin{cases} \frac{\zeta_c \exp(-\zeta_c(t-t_c-0.5\Delta_c))}{(1+\exp(-\zeta_c(t-t_c-0.5\Delta_c)))^2} R\Phi_{SS}(T, E_{AFC}, E_{DFC}, T_{HFC}) & \text{if } t > t_c \text{ and } t < t_c + \Delta_c \pmod{365} \\ 0 & \text{otherwise} \end{cases} \quad (14)$$

2.2.5 Ingestion

The different cod stages represented by index *'j'* have different intake rates of different resources, during their life they feed on zooplankton '*z*', small benthos '*b*', large benthos '*bl*', and fish '*f*' which is herring and cod. The ingestion rate of herring and cod is first calculated for each herring cohort '*i*' and cod stage '*k*', thereafter the total ingestion for herring '*h*' and for cod '*k*' is calculated.

The general formula for ingestion by cod used in this model is given in Equation 15. The intake rates of these resources follow a type II functional response, and depend on the preference for a specific resource ($p_{prey,j}$), handling time (h_j), attack rate ($a_{prey,j}$), and consumption size preference (s_{ij}) for herring with size l_i by cod stage j and (s_{kj}) for cod with representative length $\overline{l_k}$ consumed by cod stage j. Equations 16-23 represent how much cod stage j eats from a certain resource.

$$I_{prey} = \frac{p_{prey}(l)a_{prey}(l)R_{prey}}{1+h\sum_{prey} p_{prey}(l)a_{prey}(l)R_{prey}} \quad (15)$$

Total ingestion

$$I_j = I_{zj} + I_{bj} + I_{blj} + I_{hj} + I_{cj} \quad (16)$$

Ingestion of zooplankton by cod stage j

$$I_{zj}(T) = \frac{p_{zj}a_{zj}(T)R_z}{1+h_j(T)[p_{zj}a_{zj}(T)R_z+p_{bj}a_{bj}(T)R_b+p_{blj}a_{blj}(T)R_{bl}+\sum_k p_{fj}s_{kj}a_{fj}(T)C_k+\sum_i s_{ij}p_{fj}a_{hj}(T)N_i w(x_i)]} \quad (17)$$

Ingestion of small benthos by cod stage j

$$I_{bj}(T) = \frac{p_{bj}a_{bj}(T)R_b}{1+h_j(T)[p_{zj}a_{zj}(T)R_z+p_{bj}a_{bj}(T)R_b+p_{blj}a_{blj}(T)R_{bl}+\sum_k p_{fj}s_{kj}a_{fj}(T)C_k+\sum_i s_{ij}p_{fj}a_{jf}(T)N_i w(x_i)]} \quad (18)$$

Ingestion of large benthos by cod stage j

$$I_{blj}(T) = \frac{p_{blj}a_{blj}(T)R_{bl}}{1+h_j(T)[p_{zj}a_{zj}(T)R_z+p_{bj}a_{bj}(T)R_b+p_{blj}a_{blj}(T)R_{bl}+\sum_k p_{fj}s_{kj}a_{fj}(T)C_k+\sum_i s_{ij}p_{fj}a_{fj}(T)N_i w(x_i)]} \quad (19)$$

Ingestion of herring in cohort i by cod stage j

$$I_{ij}(T) = \frac{p_{fj}s_{ij}a_{fj}(T)N_i}{1+h_j(T)[p_{zj}a_{zj}(T)R_z+p_{bj}a_{bj}(T)R_b+p_{blj}a_{blj}(T)R_{bl}+\sum_k p_{fj}s_{kj}a_{fj}(T)C_k+\sum_i s_{ij}p_{fj}a_{fj}(T)N_i w(x_i)]} \quad (20)$$

Ingestion of cod in stage k by cod stage j

$$I_{kj}(T) = \frac{p_{fj} s_{kj} a_{fj}(T) C_k}{1+h_j(T)\left[p_{zj} a_{zj}(T) R_z + p_{bj} a_{bj}(T) R_b + p_{blj} a_{blj}(T) R_{bl} + \sum_k p_{fj} s_{kj} a_{fj}(T) C_k + \sum_i s_{ij} p_{fj} a_{fj}(T) N_i w(x_i)\right]} \quad (21)$$

Total herring ingestion by cod stage j

$$I_{hj}(x,T) = \sum_i I_{ij}(T)\, w(x_i) \quad (22)$$

Total cod ingestion by cod stage j

$$I_{cj}(x,T) = \sum_k I_{kj}(T) \quad (23)$$

The relative preference for a prey type of a cod of length l is given by $p_{prey}(l)$ (Eq. 24). This assumes that prey searching is only done for a single prey type at a time and that digestion is limited by all consumed prey types. The relative preference is simply the preference for the particular prey type as a proportion out of all the four prey types (zooplankton, small benthos, large benthos, fish).

$$p_{prey}(l) = \frac{p_{prey}(l)}{\sum_{prey} p_{prey}(l)} \quad (24)$$

The size-dependence of the prey preference $p_{prey}(l)$ was based on cod stomach data (Lindmark et al. 2025). Based on this data I assumed that: (1) preferences for zooplankton are an exponentially declining function of cod length, (2) preferences for small benthos are logistically declining, and (3) preferences for large benthos and for fish are 0 at sizes smaller than a minimum length of cod, and an increasing logistic function of length above that size.

$$p_z(l) = s_{1z} e^{-s_{2z} l} \quad (25)$$

$$p_b(l) = s_{minb} + \frac{s_{maxb} - s_{minb}}{1 + e^{-\zeta_b * (L - L_{Hb})}} \quad (26)$$

$$p_{bl}(l) = \begin{cases} 0, l < l_{minbl} \\ \frac{s_{maxbl}}{1 + e^{-\zeta_{bl} * (L - L_{Hbl})}} \end{cases} \quad (27)$$

$$p_f(l) = \begin{cases} 0, l < l_{minf} \\ \frac{s_{maxf}}{1 + e^{-\zeta_f * (L - L_{Hf})}} \end{cases} \quad (28)$$

Cod stage 1 does not eat large benthos and herring, therefore these values are put to zero:

$$\begin{cases} 0 & if\ l_{blj}\ and\ l_{fj} < 15 \\ p_{prey}(l) = \frac{p_{prey}(l)}{\sum_{prey} p_{prey}(l)} & otherwise \end{cases} \quad (29)$$

The consumption size preferences for herring (s_{ij}) and cod (s_{kj}) of cod in stage *j* are calculated with the Andersen-Ursin suitability function (Andersen & Ursin 1977; Ursin 1973). It is based on the minimum (Ω_{min}) and maximum (Ω_{max}) fish prey/predator length ratio, the length of herring (l_i) or representative length of cod ($\overline{l_k}$) and the representative length of cod ($\overline{l_j}$).

$$s_{ij} = \begin{cases} \frac{l_i - \Omega_{min}\overline{l_j}}{(\Omega_{opt}-\Omega_{min})\overline{l_j}} \text{ if } \Omega_{min}\overline{l_j} < l_i < \Omega_{opt}\overline{l_j} \\ \frac{\Omega_{max}\overline{l_j} - l_i}{(\Omega_{max}-\Omega_{opt})\overline{l_j}} \text{ if } \Omega_{opt}\overline{l_j} < l_i < \Omega_{max}\overline{l_j} \\ 0 \text{ otherwise} \end{cases} \quad (30)$$

$$s_{kj} = \begin{cases} \frac{\overline{l_k} - \Omega_{min}\overline{l_j}}{(\Omega_{opt}-\Omega_{min})\overline{l_j}} \; if \; \Omega_{min}\overline{l_j} < \overline{l_k} < \Omega_{opt}\overline{l_j} \\ \frac{\Omega_{max}\overline{l_j} - \overline{l_k}}{(\Omega_{max}-\Omega_{opt})\overline{l_j}} \; if \; \Omega_{opt}\overline{l_j} < \overline{l_k} < \Omega_{max}\overline{l_j} \\ 0 \; otherwise \end{cases} \quad (31)$$

The handling time by cod (h_j) scales allometrically with weight and depends on temperature. Handling time is assumed inversely correlated with gastric evacuation rate, which follows the Sharpe Schoolfield function. Handling time therefore is inversely hump-shaped temperature dependent, with shortest handling time at an optimum temperature.

$$h_j(T) = \frac{d_{1c}\overline{w_j}^{d_{2c}}}{\Phi_{SS}(T, E_{AHC}, E_{DHC}, T_{HHC})} \quad (32)$$

The attack rate on zooplankton increases with cod representative weight, up to a weight at optimal attack rate on zooplankton (w_{optc}) after which it decreases again. In contrast, the attack rates on small benthos, large benthos and fish all increase allometrically with cod representative weight. The attack rates follow a temperature-dependent Arrhenius function, in which the activation energy is dependent on the cod representative weight.

$$a_{zj}(T) = \Phi_{Arr}\left(T, E_{AM} + E_{iM}\ln\left(\overline{w_j}\right)\right) A_{maxc}\left[\frac{\overline{w_j}}{w_{optc}}\exp\left(1 - \frac{\overline{w_j}}{w_{optc}}\right)\right]^{\alpha_c} \quad (33)$$

$$a_{bj}(T) = \Phi_{Arr}\left(T, E_{AM} + E_{iM}\ln\left(\overline{w_j}\right)\right) b_{1cb}\overline{w_j}^{b_{2cb}} \quad (34)$$

$$a_{blj}(T) = \Phi_{Arr}\left(T, E_{AM} + E_{iM}\ln\left(\overline{w_j}\right)\right) b_{1cbl}\overline{w_j}^{b_{2cbl}} \quad (35)$$

$$a_{fj}(T) = \Phi_{Arr}\left(T, E_{AM} + E_{iM}\ln\left(\overline{w_j}\right)\right) b_{1cf}\overline{w_j}^{b_{2cf}} \quad (36)$$

2.2.6 Mortality

The biomass in a cod stage decreases due to mortality. Cod mortality consists of size independent background mortality (μ_0), size specific background mortality (μ_{sizej}), size specific fishing mortality (μ_{fishj}), and starvation mortality due to cannibalism (μ_{canj}). Size specific mortality declines exponentially with body size,

while fisheries mortality increases with size following a sigmoidal function. The cod eggs and larvae also experience background mortality dependent on temperature, this is incorporated into the transition from the egg buffer to the first cod stage (F_c) in Equation 14.

$$\mu_j = \mu_0 + \mu_{sizej} + \mu_{fishj} + \mu_{canj} \quad (37)$$

$$\mu_{sizej} = \mu_{wc}\exp(-\frac{\overline{l_j}}{l_{\mu c}}) \quad (38)$$

$$\mu_{fishj} = \begin{cases} 0 & if\ l(x) < L_{fminc} \\ \frac{\mu_{fc}}{1+\exp(-\zeta_{fc}(\mathrm{L_j}-\mathrm{L}_{Hfc}))} & if\ l(x) \geq L_{fminc} \end{cases} \quad (39)$$

$$\mu_{canj} = \sum_k I_{kj}(T) \quad (40)$$

2.2.7 Resource dynamics

The dynamics of the resource communities are modelled using semi-chemostat dynamics, they are formulated in terms of productivity (P) and losses (r). The productivity of the resource communities depends on temperature following the Sharp-Schoolfield equation. Zooplankton productivity decreases with increasing light intensity (Q), approaching a minimum fraction (Γ) along a sigmoidal curve. The loss of resources depends on temperature through the Arrhenius function. Zooplankton and small benthos are consumed by both cod and herring, while large benthos and herring are only consumed by cod. N_i represents the number of herring individuals in a cohort.

$$\frac{dR_z}{dt} = \Phi_{SS}(T, E_{AP}, E_{DP}, T_{HP})\left[\Gamma - \frac{1-\Gamma}{1+\exp(-\zeta_l(Q-Q_H))}\right]P_z - \Phi_{Arr}(T, E_{AR})\, r_z R_z - \sum_i I_z(T)\ N_i - \sum_j I_{zj}(T) C_j \quad (38)$$

$$\frac{dR_b}{dt} = \Phi_{SS}(T, E_{AP}, E_{DP}, T_{HP})\, P_b - \Phi_{Arr}(T, E_{AR})\, r_b R_b - \sum_i I_b(T)\ N_i - \sum_j I_{bj}(T) C_j \quad (39)$$

$$\frac{dR_{bl}}{dt} = \Phi_{SS}(T, E_{AP}, E_{DP}, T_{HP})\, P_{bl} - \Phi_{Arr}(T, E_{AR})\, r_{bl} R_{bl} - \sum_j I_{blj}(T) C_j \quad (40)$$

The total mortality for each herring cohort is the only formula adjusted for the herring dynamics in the new model, all other equations for herring are as in Croll et al. (submitted). The predation by cod on a specific herring cohort is incorporated into this formula in my model.

$$\frac{dN_i}{dt} = \begin{cases} -\mu_{size} N_i & if\ a_i < 0 \\ -\left[\mu_0 + \mu_{size}(x) + \mu_{fish}(x) + \mu_{starv}(x, y)\right]N_i - \sum_j I_{ij} C_i & if\ a_i \geq 0 \end{cases} \quad (41)$$

The formulas for the herring model can be found in appendix in Table A1 (Table reproduced from Croll et al. (Submitted). An overview of the formulas for the cod-herring model can also be found in appendix (Table A2).

2.3 Parameterisation

2.3.1 Length-limits of cod stages

The maximum length of the first cod stage was chosen as the length at which they begin to eat large benthos and herring. This value was based on the Baltic cod stomach data from Lindmark et al. (2025). This data has been collected by national institutes over the past decades. The next stage limit distinguished juveniles from adults, and the maximum size of stage two is therefore equal to the maturation size. Vainikka et al. (2009) demonstrated that the maturation size for two- to four-year-old cod is around 32 cm, however there was a clear downward trend in their graph. Therefore, I have chosen to take the length for maturation age at 30 cm instead of 32 cm to have a better representation of current maturation size. To understand how temperature affects different cod size stages, I divided the adult cod stage into a small, large and largest adult stage. The maximum length for stage three was chosen to divide stage three and four into more or less equal stages in terms of their representative lengths. Stage five is the final stage that the cod can reach. As these cod cannot grow, they have the maximum length for cod stage four (set to be 100 cm). This was also based on the cod stomach data from Lindmark et al. (2025). The parameters for size weight scalers are based on the paper from Coull et al. (1989), which is based on Atlantic cod.

2.3.2 Preference in the diet of cod

The parameters for the preference functions for small benthos, large benthos and fish (Eq. 26-28) were fitted to the Baltic cod stomach data from Lindmark et al. (2025) (Fig. A1). The preferences for each resource as a function of the cod length are given in Figure A2.

The preference for each cod stage is calculated based on its representative length (Table A3). The relative preference value for each prey of each cod stage was then calculated by dividing it by the sum of all preferences of that cod stage, such that total preference across all prey equals 1 for each stage. Stage one does not eat large benthos and fish, therefore, the values for s and f of that stage were set to zero (Eq. 29) before relative preferences were calculated. The final preference values are presented in Table A4.

2.3.3 Cod attack rate

The parameters for cod attack rate on zooplankton were based on perch data from Byström & García-Berthou (1999). The parameters for the attack rates of small and large benthos are also based on perch data and come from van Leeuwen et al. (2013). Perch is comparable with cod, as they are both piscivores that rely on benthos and undergo multiple ontogenetic niche shifts (Hjelm et al. 2000). Therefore, parameter values for perch can be used for cod parameterisation. I assumed the same attack rate scaler for small and large benthos. The reasoning behind using the same values for both small and large benthos is that I assumed that it depends only on the swimming speed of the fish, which in turn depends on the length of the fish and not on the prey species. The parameters for the optimum attack rate on fish are based on Claessen et al. (2000), which are also based on perch data.

2.3.4 Prey-predator size ratio

The parameter values for minimum/optimum/maximum prey-predator size ratio are based on Kulatska et al. (2019). I took the average of the prey-predator ratio for the different Baltic cod sizes for herring and chose those values as my parameter values. Table A4 contains the values that I abstracted from the graph from Kulatska et al. (2019). Using these values I made Figure A3, which represents predator-prey length suitability for different cod sizes. Figure A4 gives the minimum/optimum/maximum prey length for a certain predator length.

2.3.5 Cod body growth

The assimilation efficiency parameter value was based on the article Peters (1983). Cod stage three and four invest a fraction (k_j) of their net biomass production in somatic growth. I assume k_3=0.8, based on van Leeuwen et al. (2008). As cod in stage four are larger, they will spend more energy on reproduction than in stage three, and I therefore assume that they spend only half as much energy on growth, with k_4=0.4.

The parameterisation for maintenance was based on a meta-analysis on measurements of fish metabolism, by Lindmark et al. (2022). In the model, maintenance of tissues has energetic costs, and these are assumed to scale proportionally with metabolic rate, this is why I use estimates for metabolism to scale them. The parameter value for mass specific activation energy was based on their meta-analysis on multiple species. The activation energy, allometric scaler and exponent for metabolism were based on experiments on Atlantic cod. A non-linear least squares regression (nls) was used to rescale the values from Lindmark et al. (2022) to fit the reference temperature of my model (Fig. A5), the

parameters I varied were ρ_{1c} and E_{AMC}. As the metabolic rate is in mg O_2/h I recalculated this to the unit of my model which is $d/g^{(1-\rho 2c)}$. I used the same conversion coefficient that Lindmark et al. (2022) used, which is "0.0608" to do a back calculation for the units. I multiplied my number by 0.0608 to come to my current value for E_{AMC}.

2.3.6 Handling time

The allometric scalers for handling time are based on Björnsson et al. (2007). He derived his values from the combination of size-specific maximum growth rate, maintenance rate and assimilation efficiency, from which he obtained the maximum rate of ingestion, with maximum growth. The parameter values for activation energy, deactivation energy and temperature of half deactivation are based on the meta-analysis from Lindmark et al. (2022). To rescale the parameter values to my model reference temperature, I first calculated the handling time for 5 °C and length 10 cm with the parameter values from van Leeuwen (2013) to obtain a point for which I then could vary the value d_{1c} so that the graph would go through this obtained point (Fig. A6).

2.3.7 Reproduction and egg survival

Based on the paper of Bleil et al. (2009), the spawning period for the eastern Baltic cod extends from June to September with a maximum occurrence in August. Therefore, I use June 1st (DOY=152) as the start date and September 30th (DOY=273) as the end date. The duration of the cod reproductive season is then 121 days. The parameter values for the egg survival were based on a graph from Peck et al. 2012 for Atlantic cod. I fitted the function for temperature-dependence of egg survival (Eq. 14) to this graph and standardised it.

2.3.8 Mortality

The parameter values for the fish mortality were obtained by doing back calculations on north-east Arctic cod data (Fig. 4; Table 2 from Kvamme & Isaksen (2004)) (Fig. A7). They obtained their data through a series of experiments with fishing hauls conducted west of Bear Island in the Barents Sea (Kvamme & Isaksen 2004). Size specific mortality parameters were based on the parameter values from Croll et al. (submitted). I thereby assume that size specific mortality of small individuals is the same for herring and cod, as it mainly represents the mortality due to predation by other species than herring and cod.

2.3.9 Optimising parametrisation

After finding the parameters, the model was then checked upon biological criteria for the reference temperature of 8.588 °C. Both cod and herring needed to survive in the model, the maximum length of herring should be between 0 and 25 cm (Berg et al. 2018). Herring maturation happens between two and three years (Parmanne et al. 1997). The maturation of cod also had to happen between two and four years (Vainikka et al. 2008); The cod also needed to have a realistic growth pattern (Fig. 7 from Mion 2021), which here is reflected in the stage durations.

To fit these criteria, I varied parameters for herring and cod. For herring, I changed the following parameters: productivity zooplankton (p_z), productivity small benthos (p_b), small benthos turnover rate (r_b), weight specific mortality constant herring (μ_w), and background mortality herring (μ_0). For cod, I chose values for productivity of large benthos (p_{bl}), large benthos turnover rate (r_{bl}), maximum fishing pressure on cod (μ_{fc}), and background mortality rate cod (μ_{0c}) such that the criteria were fulfilled. With the new parameter values, cod stage durations are 2.1 years (stage 1), 1.7 years (stage 2), 3.2 years (stage 3), and 9.8 years (stage 4). The parameter values for the herring with the mentioned adjustments are given in Table A5 (Table reproduced from Croll et al. submitted) and parameter values for the cod are given in Table A6.

3. Results

3.1 Description of population dynamics of herring and cod under warming

Warming changes the population dynamics of cod and herring, it alters biomass levels, changes the population cycle amplitude and period, and ultimately leads to the extinction of both species (Fig. 1). Herring biomass increases with temperature. Following cod extinction, herring biomass increases markedly, particularly in the juvenile stages (Fig. A8). With warming the biomass composition of cod changes greatly as juvenile biomass increases less than adults, and large adult biomass increases sharply before it declines, and cod goes extinct (Fig. 1b). Warming also influences the cyclicity of cod and herring (Fig. 1). For herring, fluctuations in cycle amplitude remain relatively stable at lower temperatures, however at higher temperatures the amplitude is greater and less regular, with biomass for juveniles or adults being zero for certain temperatures (Fig. 1a). In contrast, warming has less influence on cycle amplitude for cod (Fig. 1b). The periodicity of the cycles is as for herring relatively stable at lower temperatures but becomes increasingly variable as temperature rises. Eventually, warming leads to extinction of both populations, with cod extinction around 17 °C, followed by herring around 21 °C. To understand the mechanisms behind these patterns, I first examined the dynamics of cod and herring at a normal central temperature of 8 °C, whereafter I examined how warming affects biomass, population cycles, and extinction. Thereafter, the extent to which the responses to warming are modified by interactions between cod and herring was investigated.

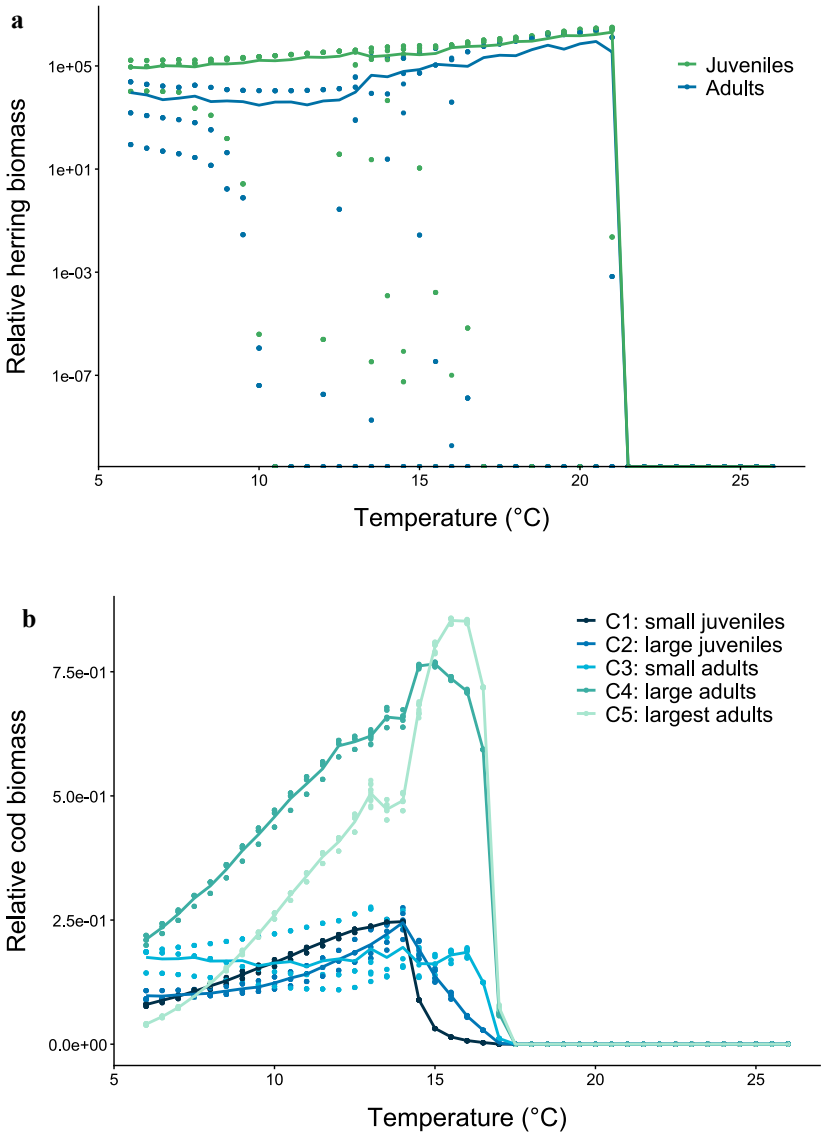


Figure 6: Bifurcation graphs of herring biomass density (a) on a log-scale and cod biomass density (b) on non-log scale as a function of temperature. The bifurcations are made between 6 and 26 °C, the used step size is 0.5 °C and the output is generated every year at the start of the reproduction period. The full line represents the average biomass while the dots represent the biomasses in each year of the period of the population cycle (for example, three dots for a given temperature means there is a 3-year cycle).

3.2 Dynamics at normal temperature

To understand why warming alters cod and herring dynamics in this way, I first compare them with their dynamics and mechanisms in an environment with a central temperature of 8 °C. Herring and cod populations cycle then with a three-year population cycle (Fig. 2). The herring population dynamic is mainly driven by competition for resources. Once every third year, herring adult biomass reaches a peak (Fig. 2c), resulting in the production of a dominant cohort, reflected in a pronounced increase in eggs and larvae during that year (Fig. 2a). This leads to an increase in juvenile biomass (Fig. 2b). The higher abundance of juveniles intensifies competition for resources, particularly zooplankton (Fig. 3). Adult biomass decreases after the birth of the dominant cohort. This is due to mortality but also due to slower maturation of juveniles, which is in turn caused by the more intense competition. The intensified competition leads to a drop in reproduction in the following years of the cycle. This in turn reduces competition, leading to higher zooplankton densities, which supports further growth. After approximately two and a half years, adult biomass rises sharply as the dominant cohort reaches maturity. Due to the higher adult biomass in synchrony with the higher resource density in summer, it is again possible to have higher reproduction, resulting in the production of a new dominant cohort, restarting the cycle. The cod cycles are mainly driven by the herring cycles, showing the prey-dependence of cod (Fig. A9). Fluctuations in invertebrate resources depend on the season, with more resources available during summer than winter, but also cycles interannually due to the consumption by herring and cod (Fig. 3, Fig. A10).

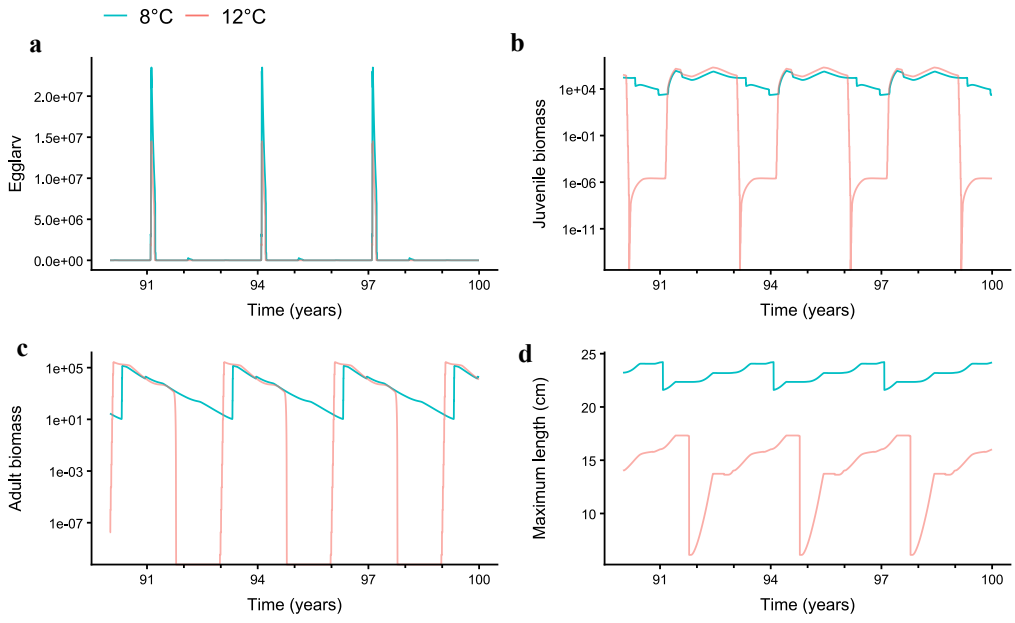


Figure 2: Variation in Egglarv (total amount of released eggs and larvae) (non-log) (a), juvenile biomass (log) (b), adult biomass (log) (c), and maximum length (non-log) (d) of herring across time (years), at 8 °C and 12 °C.

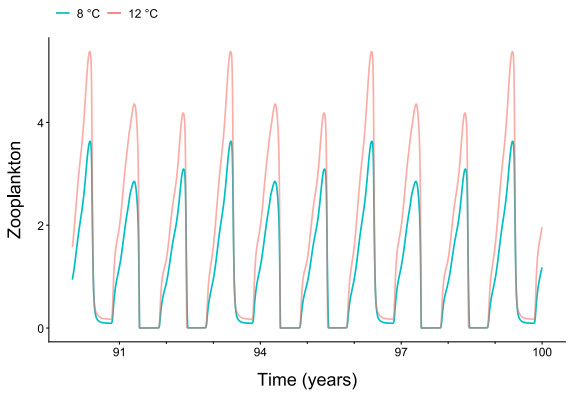


Figure 7: Zooplankton density (non-log) across time (year), at 8 °C and 12 °C.

3.3 Changes in biomass levels

Warming alters the biomass of cod and herring. Juvenile herring biomass increases with warming. After the extinction of cod, herring biomass increases substantially, especially for juveniles (Fig. 1a). The absence of predation pressure from cod makes this increase possible. The increase in biomass with temperature is linked to a higher abundance of zooplankton and small benthos for higher temperatures during the summer (Fig. A10). The biomasses of both herring and cod reach a peak right before extinction (Fig. 1). For cod, biomass increases slightly for juveniles and more sharply for large adults with warming up to intermediate temperatures (here 14 °C; Fig. 1b). In contrast, the small adult cod remains relatively stable with rising temperatures (Fig. 1b). Availability of prey that is unique to cod, that is the large benthos and herring, increase with temperature (Fig. A10). This might explain the larger increase in large cod adults in comparison to cod juveniles who feed more on zooplankton and small benthos and thus compete with herring. There appears to be a transition in cod biomass around 14 °C (Fig. 1b). Although egg production of cod is higher at 15 °C compared to 12 °C, juvenile biomass decreases instead of increases after 14 °C (Fig. A11). This pattern could likely be caused by a lower egg survival of cod with increasing temperatures (Fig. A12). In contrast, large adult cod and especially the largest cod continue to increase with temperature up to 16 °C, after which it sharply decreases and becomes extinct (Fig. 1b). The increase in biomass production is likely due to higher resource availability (Fig. A13). In addition, stage duration for the small and large adults decreases with temperature, indicating faster growth, which may further contribute to the accumulation of biomass in the larger size classes (Fig. A14).

3.4 Warming changes cycle amplitudes and periodicity

Another effect of warming is that it changes the amplitude of population cycles (Fig. 1). This change in amplitude is visible at a temperature of 10 °C for herring (Fig. 1a). Therefore, to understand what causes this shift in cycle amplitude, I compare the cod and herring dynamics at 8 °C and 12 °C (Fig. 2). Increasing temperature enforces the dominant herring cohort; it grows faster due to increased resource availability and increased consumption rate. The faster growth allows juveniles to reach larger sizes more quickly, thereby reducing their size-dependent mortality. As a result, more individuals survive and juvenile and adult herring peak biomasses are higher (Fig. 2, Fig. A15). This leads to increased competition for resources, which lowers availability of zooplankton and small benthos (Fig. A10). At the warmer temperature, adult herring seem to experience starvation mortality, because a steep drop in zooplankton is directly followed by the complete disappearance of all adults (Fig. 2). Due to the starvation of adults and the slow growth caused by competition, all individuals remain below the maturation length, which is 14 cm, for two years (Fig. 2). Consequently, reproduction occurs only once every third year for herring.

Warming influences not only the amplitude of the cycle but also its periodicity. For example, the cycle duration changes from three to five years, as temperature increases from 12 °C to 15 °C (Fig. 1, Fig. A16). Warming increases resource availability and therefore it reduces competition (Fig. A13). Herring can then grow faster as there are more resources per capita, which makes it possible for them to mature in two years instead of three. The next reproduction follows three years later and is less dominant, after which a more dominant cohort is born two years later, thereby restarting the five-year cycle (Fig. A16).

3.5 Extinction of cod and herring

Warming ultimately leads to the extinction of both cod and herring (Fig. 1). The extinction of cod in the model is probably caused by a combination of low egg survival and too high energy losses during the summer period (Fig. 4), resulting in elevated mortality. There is a shift in net energy gained with temperature across cod stages (Fig. A17). At lower temperatures (e.g., 8 °C), both maintenance costs and food intake are high during summer and net energy gain is higher in summer than in winter (Fig. 4a). With warming this seasonal pattern changes. Around 12 °C, food intake is instead lower during summer than during winter, causing the net energy gain for some stages to be negative during summer (Fig. 4b). This could be a consequence of how temperature affects handling time. Handling time describes the time needed to consume a prey, which first decreases and later increases with higher temperatures (Fig. A18). During summer, cod

therefore has even lower food intake at 17 °C than at 12 °C, as well as higher maintenance costs (Fig. 4b,c, Fig. A17). As a result, the net energy gain is more negative in summer and remains negative for longer periods. This lowers cod biomass significantly and likely contributes to the extinction of the cod. Prior to the extinction, cod loses its regulatory influence on herring dynamics. This is reflected in a shift in cycle duration from approximately eight years at 16 °C to three years at 17 °C (Fig. A19). This loss of control is most likely due to the decline in cod biomass to very low levels, reducing its impact as a predator within the system.

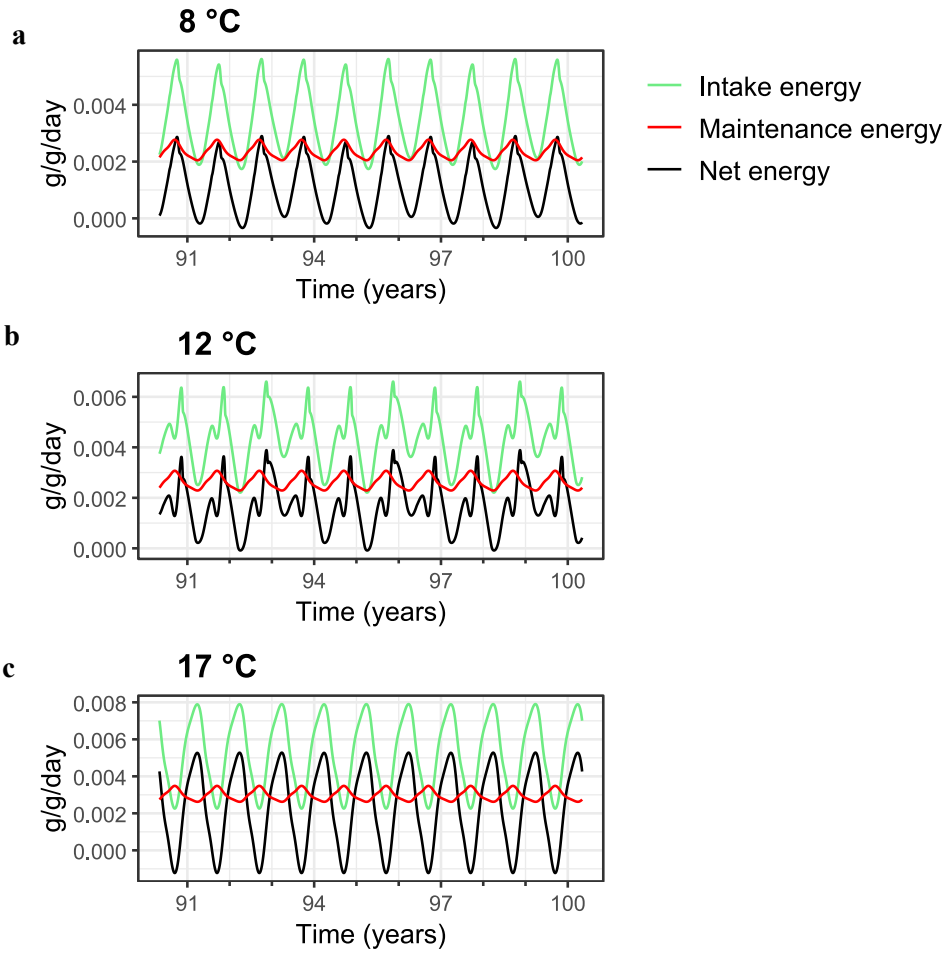


Figure 8: Variation in intake energy, maintenance energy, net energy gain across time (years) for large adult cod (stage 4) at 8 °C (a), 12 °C (b) and 17 °C (c).

Herring in the model could go extinct due to too low egg survival, too high predation, too low condition for reproduction or too slow growth rates to reach maturity. However, egg survival remains sufficiently high at elevated temperatures (Fig. A20), and predation by cod cannot explain the extinction, as cod is already extinct at these temperatures (Fig. 1). A remarkable change with warming that precedes extinction is the shift in cycle length from three to four years (Fig. A21), this indicates a slowdown in growth. The handling time of herring decreases until around the point of extinction, after which it increases sharply (Fig. A22). The combination of an increase in handling time with higher metabolism under warming could have caused the net energy gain to decrease, resulting in slower growth. Because of the slow growth rate, individuals need a very long time to reach the maturation size. Furthermore, when net energy gain is negative, individuals could starve and their condition could become too low to be able to reproduce. The combination of low growth rates and low condition is therefore likely to have ultimately led to the extinction of herring in this model. Like cod, herring likely suffered more during summer as higher temperatures likely caused a stronger net energy reduction, leading to their extinction.

3.6 Cod and herring interactions affect their responses to warming

Does the effect of warming on herring depend on cod and vice versa? I investigated this question by comparing the herring dynamics with and without cod in the model, and the other way around. In the presence of cod, warming shifts the periodicity and structure of herring population cycles in ways that would not occur when there is no cod. This is because cod predation affects intraspecific competition among herring. At low temperatures (here 8 °C), herring reproduces every year when cod is present and only once every third year when cod is absent (Fig. A23). In the absence of cod, warming (e.g. 15 °C) leads to a three-year cycle in herring (Fig. A24). In contrast, warming leads to a five-year cycle when cod is present, which is a combination of reproduction after two years, followed by reproduction after three years (Fig. A24). This difference in warming responses occurs because predation by cod increases juvenile mortality in herring, which reduces competition for resources among survivors. The lower competition prevents starvation of adults and stimulates growth, leading to higher reproduction in years when the non-dominant cohorts are born. The effect of the dominant cohort is thus reduced when cod is present. Higher temperature increases resource availability (Fig. A13). In combination with the stimulating herring growth effects caused by cod predation, this leads to earlier maturation, such that in warm environments herring matures once in two years instead of three in the five-year cycle.

How cod responds to warming is also influenced by its interactions with herring. In the absence of herring, warming does not change cod cycles, only its biomass. With herring present, the cod cycle dynamics change with warming. In addition, herring influences how cod biomass changes with warming (Fig. A25-26). Without herring, cod has a one-year cycle driven primarily by seasonality, and warming does not alter this periodicity (Fig. A25-26). In contrast, when both species are included in the model warming shifts populations from a three-year cycle (at 8 °C, Fig. A25) to a five-year cycle (at 15 °C, Fig. A26). Since herring also displays a three-year cycle at 8 °C in the absence of cod, this suggests that herring largely determines the cycle length of the interacting cod and herring populations. Under warming, the biomass of the small juveniles of cod increases more sharply in the absence of herring than when herring is present. At lower temperatures, there is more competition between herring and the small juveniles for the same resources, leading to lower biomass when herring is present compared to when it is absent (Fig. A25). At high temperatures, resources increase (Fig. A13), which reduces competition. Moreover, cod densities increase with higher temperatures and therefore their predation pressure. Predation pressure on cod's own juveniles is stronger without herring, therefore the biomass of the small cod juveniles is higher in the presence of herring for higher temperatures (Fig. A26). The biomass level of the large cod stages increases with warming both in the presence and absence of herring. When herring is present, warming increases the biomass of the largest cod stage the most (Fig. A25-26). As temperatures increase, so does herring biomass. Higher resource availability leads to an increase in cod biomass and faster growth rates, i.e. reduced stage duration of stage four as they grow into the largest cod stage. The biomass in the largest cod stage could therefore increase even more with warming in the presence of herring than when herring is absent.

4. Discussion

Warming affects population dynamics of cod and herring in a seasonal environment through different mechanisms. First, warming alters biomass levels. Warming results in an increase in biomass of cod and herring until a certain point, after which their biomasses decline sharply before extinction. Second, warming alters population cycle amplitude and periodicity. Lastly, warming ultimately leads to the extinction of first cod and then herring. Seasonality mainly seems to influence cod extinction and most likely also contributes to herring extinction. For the other responses to warming, seasonality does not seem to have a major influence. Taking seasonality into account is thus likely most important when studying extinction due to warming. Furthermore, the presence of cod alters the effects of warming on herring, and the other way around. In the presence of cod, warming changes the periodicity and structure of herring population cycles in a different way than without cod. Conversely, the cod biomass levels change differently with temperature when cod interacts with herring. Taking species interactions into account is thus important when predicting the effects of warming on population dynamics.

Under warming, I found that biomass of both species increases with temperature until it declines sharply before extinction. The increase in biomass is likely caused by higher resource availability at elevated temperatures. Increased resource biomass raises the energy available for consumers and thereby increases consumer biomass (Gilbert et al. 2014). Lindmark et al. (2019) found that in most temperature-scaling scenarios predator biomass density declined with warming, this could happen gradually or in the form of a collapse. However, they also found that biomass can increase with warming under the condition that the basal resource density does not decrease with temperature, which implies that the resource turnover rate must increase faster with temperature than feeding and metabolic rates. This condition is met in my model, as the resources continue to increase with temperature. Furthermore, Lindmark et al. (2019) found that biomass decline of predators with warming is not always gradual but can be sudden. They predicted that biomass decline is non-gradual when predators mainly feed on smaller consumers, which is the case in my model. Although I also find a sudden decline in biomass, the mechanisms behind that are slightly different. This is mainly because in the model of Lindmark et al. (2019) the predator only feeds on one prey and not on any additional resources, whereas in my model cod feed on herring, cod and invertebrate prey. Although previous studies suggested that biomass can both decrease and increase with warming (Lindmark et al. 2019; Gilbert et al. 2014), I found that in a seasonal environment with sufficient resource availability, biomasses increase with temperature and then decline rapidly before extinction.

Population cycles' amplitude and periodicity change under warming in my model, which is most likely caused by changes in competition caused by warming. Ohlberger et al. (2011) also found that warming can cause competition-driven generation cycles. Unlike Ohlberger et al. (2011), who found that warming shifts dynamics from stable equilibrium dynamics to generation cycles, generation cycles were already present at lower temperatures in my model. Ohlberger et al. (2011) found that warming increases energy gain faster for smaller than for larger individuals. This reinforces the competitive advantage of small individuals over larger ones, which enhances mechanisms that strengthen generation cycles. Due to the competitive advantage of smaller individuals with warming, dominant cohorts can become stronger, thereby altering a cycle's amplitude, which is also found in my results. I had a similar negative feedback loop in which increased reproduction due to warming results in higher competition, while higher competition results in a decrease in reproduction, as Croll et al. (submitted) found. Although not studying effects of warming, Van Leeuwen et al. (2014) similarly found that cyclic dynamics are driven by size-dependent scaling of net energy production, which is more favourable for small individuals (Hjelm & Persson 2001; Huss et al. 2012). That is, the cycles are driven by juveniles' competitive ability. I also found that the cohort cycles were juvenile-driven, which also has been found previously (Croll et al. submitted; Ohlberger et al. 2011). Moreover, they found that these cyclic dynamics also occur due to the discrete reproduction event. As in Van Leeuwen et al. (2014), reproduction in my model also did not occur continuously but only during a restricted reproductive season. Another factor that is known to affect cohort cycle dynamics is size-dependent mortality (van Kooten et al. 2007). Huss et al. (2013) found that size-dependent mortality strongly influences the periodicity of these cycles. This however was not tested in my model. My results support previous findings that warming can alter cycles amplitude and periodicity through changing competition and show that this holds under a seasonal environment.

Ultimately, warming leads to the extinction of cod and herring. Most likely, the cod went extinct in my model due to an energetic mismatch. This occurs because for high temperatures the metabolic demand becomes too large to be met with the decreased food intake rates that occur due to warming limiting cod handling time. During summer this mismatch is more pronounced due to the higher temperatures. For herring, I found that their extinction was likely due to a combination of slow growth and starvation induced by higher temperatures. This mechanism is consistent with Fussmann et al. (2014), who suggested that warming can cause extinction when metabolic demands increase faster than their predation rates. Cod get extinct at a lower temperature than herring in my model, which is also consistent with what other authors found for predators and their prey (Gillooly et al. 2001; Lindmark et al. 2019). As cod has a larger average body size, it has

higher energetic costs that also increase faster with temperature than for smaller individuals (Lindmark et al. 2022), resulting in slower growth with increasing temperature compared to herring (Brown et al. 2004; Lindmark et al. 2019; Gilbert et al. 2014). Buba et al. (2022) found that handling time decreases with increasing temperature for smaller predators but increases for larger predators. A similar pattern occurs in my model, where handling time decreased with temperature for herring until the point where they go extinct (whereafter it increased), but increased for cod already at lower temperatures. This likely reduced feeding efficiency in cod under warming conditions, reinforcing the energetic mismatch that led to their earlier extinction. My findings indicate that the combination of seasonal variation and size-dependent energy mismatch may play an important role in understanding species persistence under warming.

Cod and herring both change each other's responses to warming. Without cod, there would be higher competition among herring juveniles, leading to more influence of the dominant cohort on herring dynamics. Lindmark et al. (2019) also found that in the absence of a predator, juveniles are competitively superior to adult consumers. This could explain the warming-induced enforcements of dominant cohorts without predators that I found. The effect of warming on cod is also influenced by the presence of herring. Herring densities increase with warming, resulting in higher resource availability for larger cod, which in turn can increase their biomass. Dee et al. (2020) found in a non-seasonal model that the effect of temperature changes when species interact can be different from the effect of temperature on a single species. Therefore, they highlight the importance of considering temperature effects in context with both intra- and interspecific interactions. Consistent with previous studies, I found that considering species interactions is important when studying effects of warming on population dynamics. I also extend previous work on warming on predator-prey dynamics by showing that this importance also holds in a seasonal environment.

My results are most influenced by three important assumptions, of which assuming there is seasonality is the most important. Furthermore, I assume that cod in addition to the resources they shared with herring has its own unique resources, large benthos and fish (including cannibalism). Lastly, I assume that mortality of juveniles and adults is not temperature dependent, only eggs and larvae are. Below I discuss each of these three assumptions. Seasonality occurs in a major part of the world and therefore influences the dynamics of many species, including Baltic cod and herring. Seasonality mainly mattered for the extinction of cod. It is likely also an important factor for the extinction of herring in my model, however this should be further investigated. My model differs from non-seasonal models by including a winter period in addition to summer dynamics. In the winter period, temperatures return to a range more favourable for species under warming, therefore ignoring this winter period could lead to overprediction

of the negative impacts of warming (Dee et al. 2020). In general, ignoring seasonality can lead to unreliable or biased estimates of population dynamics (Xia et al. 2021; Dee et al. 2020). Therefore, including seasonality likely improves the reliability of my results for temperature systems exhibiting temperature seasons.

Another important assumption I made is that cod feed on a separate exclusive resource, large benthos (*Saduria entomon*). As a consequence, cod have a higher chance of survival in our model. Van Leeuwen et al. (2014) showed that an additional resource is an energy boost for the predator and increases the predator's potential for top-down control of prey. The outcome of my results for cod is therefore more positive than in analyses and models without the consideration of this extra resource. Cod does not only have the large benthos as an extra resource in addition to feeding on herring, but also its own young. I assumed cannibalism of cod in my model, as it influences population dynamics (Claessen et al. 2000). Sparholt (1994) and Neuenfeldt & Köster (2000) stated that cannibalism is important to take into account since it has been shown to cause considerable juvenile mortality. By assuming these extra resources that cod can feed upon, it is possible for the cod to persist without herring in the model. The added extra resources unique to cod result in for example other extinction mechanisms, than when predators feed only on a single prey (Lindmark et al. 2019; Thunell et al. 2021). For example, Thunell et al. (2021) found that warming in intraguild predation can lead to extinction of the predator through a loss of cultivation mechanisms. Although cod and herring also form an intraguild predation in my model, cod also feed on exclusive resources. This could have reduced the effect of cultivation mechanisms in my model, therefore this did not led to cod extinction.

In my model, I assumed that maturation size remained constant with increasing temperatures. However, Niu et al. (2023) found that warming can lead to maturation at a smaller size. This response could help populations adjust to changing environmental conditions. Therefore, allowing maturation size to vary with temperature could have led to a more positive result of species persistence under warming. Furthermore, I assumed that mortality of juveniles and adults is not directly temperature dependent and only mortality of eggs and larvae depends on temperature. However, previous studies have demonstrated that warming may indirectly increase fish mortality by influencing other environmental factors, such as eutrophication and hypoxia (Bossier et al. 2021; Neumann 2010; Rosciszewski-Dodgson & Cirella 2024). Warming reinforces eutrophication, which in turn drives harmful algal blooms (Neumann 2010; Zillé & Conley 2010). These blooms further contribute to oxygen depletion, thereby increasing hypoxia (Hasan et al. 2023). Hypoxia itself is also stimulated through warming and increases fish vulnerability to disease and reduces survivability (Díaz & Rosenberg 2011). As mortality changes competitive behaviour, my results could have been slightly different if these indirectly temperature-dependent effects on mortality had been

included. Not including temperature dependent mortality could therefore lead to an overestimation of species persistence. However, it is very hard to know which factors contribute how much to a certain form of mortality. To not overcomplicate my model, I have decided to leave these extra factors out of my model.

Similar patterns to those I found for cod and herring in the Baltic Sea under warming can be generalised to different systems and species. The Baltic Sea system was modelled in a general way, without including specific characteristics of the Baltic Sea, such as salinity. Therefore, patterns occurring under warming may be generalised to other water bodies, like oceans and lakes located in the temperate zone, i.e. exhibiting seasonality. Furthermore, this model incorporates several ecological processes that are common among fish species. By considering two prey communities for herring, and four prey communities for cod, an ontogenetic shift can occur during their lifetime. This is a common and important phenomenon among fish species (Mittelbach & Persson 1998, Nakazawa 2015, Sánchez-Hernández et al. 2019). Additionally, for most fish species, the shapes of temperature dependence curves of physiological processes are very similar (Bruno et al. 2015, Lindmark et al. 2022, Pörtner & Peck 2010, Volkoff & Rønnestad 2020). These similarities suggest that the responses of cod and herring dynamics to warming may be generalisable to predator-prey dynamics under warming across a broad range of fish species living in seasonal environments.

In conclusion, in this study I investigated how patterns and mechanisms of the dynamics of predator and prey fish change when temperature rises using Baltic cod and herring as a case study. This study showed that warming in a seasonal environment initially leads to an increase in biomass, followed by a rapid decline before extinction. The results further showed that warming-driven changes in cycles amplitude and periodicity, as reported in studies ignoring seasonality, are also found when including seasonality. Moreover, seasonal variation combined with size-dependent energy mismatch can lead to extinction. Importantly, I found that predator-prey interactions alter how warming affects population dynamics. It is thus important to take both species interactions and seasonality into account when studying the effects of warming on population dynamics. The model includes general ecological and temperature-dependent processes common among many fish species, therefore the results can be generalised to other predator-prey systems in the temperate zone. Understanding how warming alters population dynamics is essential for improving ecological predictions of how climate warming affects species interactions, population stability, and persistence. Further research is needed to investigate the role of seasonality in shaping warming-driven population dynamics, particularly its contribution to species extinction. In addition, from a management perspective it would be valuable to study the combined effects of warming and fishing pressure on population dynamics.

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Popular science summary

Global warming affects species and ecosystems worldwide, in some cases with catastrophic consequences. This is also the case for cod and herring in the Baltic Sea. The Baltic Sea is a climate sensitive ecosystem, which has an ongoing change of sea surface temperature of 0.5 °C per decade. The Baltic Sea is surrounded by 85 million inhabitants, making it one of the most exploited marine habitats. Both cod and herring have been heavily overfished. This even led to the collapse of the Baltic cod population. Currently, the cod population is so low in numbers that there is a fish closure on cod since 2019, it is still allowed to fish for herring despite a recommended closure. Warming further increases stress on these already suffering populations. It is important to study the consequences of warming on cod and herring to understand how they will react to this stressor. This is so that we can change our fisheries policies to help fish populations under warming and to prevent species from going extinct.

Warming affects biomass and size of individuals. This in turn changes the interactions between predator and prey. In this study, these dynamics are modelled mathematically for different temperatures. The model includes seasonality and temperature dependent fish physiology and feeding patterns to understand how fish respond to warming in a seasonal environment. The results show that the predator is more vulnerable to warming than its prey, as they go extinct at lower temperatures. For smaller temperature elevations, temperature-related disturbances already occurred. For example, warming can lead to a disruption in herring reproduction. For an average temperature of 8 °C, herring reproduces every year, while warming with +2 °C can cause herring to reproduce only once every three years. Furthermore, the results also showed that it is important to take both species interactions as well as seasonality into account when studying the effect of warming on population dynamics. The patterns observed under warming found in this model can be generalised to other predator-prey systems living in seasonal environments, such as found in the temperate zone. To improve ecological predictions of how global warming affects species, it is important to understand how warming alters population dynamics. With ongoing climate change, it is increasingly important to conduct more research to understand how fish populations respond to increasing temperatures, so that they can be better preserved under a warming climate.

Appendix

1. Methods

1.1 Herring formulas

Table A1: Formulas for herring model (Table reproduced from Croll et al. submitted)

1. Formulas for the continuous dynamics of the model

Temperature and light	
Temperature curve	$T(t) = T_c + T_a(t)\, sin\left(\frac{2\pi}{365}[\, t\, -\, T_s(t)]\right)$
Temperature amplitude	$T_a(t) = \, a_c + \, a_a \, sin\left(\frac{2\,\pi}{365}[\, t\, -\, a_s]\right)$
Temperature shift	$T_s(t) = s_c + \, s_a \, sin\left(\frac{2\,\pi}{365}[\, t\, -\, s_s]\right)$
Light intensity	$Q(t) = \, Q_c + \, Q_a \, sin\left(\frac{2\pi}{365}[\, t\, -\, Q_s]\right)$
Arrhenius equation	$\Phi_{Arr}(T, E_A) = \, exp\left(-\frac{E_A}{k_B}\left[\frac{1}{T} - \frac{1}{T_r}\right]\right)$
Sharpe-Schoolfield equation	$\Phi_{SS}(T, E_A, E_D, T_H) = \frac{exp\left(-\frac{E_A}{k_B}\left[\frac{1}{T} - \frac{1}{T_r}\right]\right)}{1 \, + \, exp\left(-\frac{k_B}{E_D}\left[\frac{1}{T} - \frac{1}{T_H}\right]\right)}$
Prey dynamics	
Zooplankton	$\frac{dR_z}{dt} = \Phi_{SS}(T, E_{AP}, E_{DP}, T_{HP})\left[\Gamma - \frac{1-\Gamma}{1 + exp(-\zeta_l[Q - Q_H])}\right]P_z - \Phi_{Arr}(T, E_{AR}) r_z R_z - \sum_i I_z(x_\mathrm{i}, T) N_\mathrm{i}$
Small benthos	$\frac{dR_b}{dt} = \, \Phi_{SS}(T, E_{AP}, E_{DP}, T_{HP}) P_b - \Phi_{Arr}(T, E_{AR}) r_b R_b - \sum_i I_b\,(x_\mathrm{i}, T) N_\mathrm{i}$
Individual herring energetics	
Weight conversion	$w(x) = [1 + q_r]x$
Length conversion	$L(x) = \lambda_1 w(x)^{\lambda_2}$
Zooplankton attack rate	$A_z(x,T) = \Phi_{Arr}\big(T, E_{AM} + E_{iM}\ln\big(w(x)\big)\big) A_{max}\left[\frac{w(x)}{w_{opt}}\exp\left(1 - \frac{w(x)}{w_{opt}}\right)\right]^{\alpha}$
Small benthos attack rate	$A_b(x,T) = \Phi_{Arr}\big(T,\ E_{AM} + E_{iM}\ln\big(w(x)\big)\big) b_1 w(x)^{b_2}$
Handling time	$H(x,T) = \frac{d_1 w(x)^{d_2}}{\Phi_{SS}(T, E_{AH}, E_{DH}, T_{HH})}$
Zoobenthos preference	$B(x) = \frac{B_{max}}{1 + \exp(-\zeta_B[L(x) - L_{HB}])}$
Zooplankton ingestion	$I_z(x,T) = \frac{[1 - B(x)]A_z(x,T)R_z}{1 + \big[[1 - B(x)]A_z(x,T)R_z + B(x)A_b(x,T)R_b\big]H(x,T)}$
Small benthos ingestion	$I_b(x,T) = \frac{B(x)A_b(x,T)R_b}{1 + \big[[1 - B(x)]A_z(x,T)R_z + B(x)A_b(x,T)R_b\big]H(x,T)}$
Maintenance costs	$E_m(x,y,T) = \Phi_{Arr}\big(T, E_{AM} + E_{iM}\ln\big(w(x)\big)\big)\rho_1[x + y]^{\rho_2}$
Growth energy	$E_g(x,y,T) = k_e[I_z(x,T) + I_b(x,T)] - E_m(x,y,T)$

Energy allocation	$f(x,y) = \begin{cases} \frac{1}{[1+q_j]q_j^2}\left[\frac{y}{x}\right]^2 & \text{if } L(x) < L_m \text{ and } \frac{y}{x} < q_j \\ \frac{1}{[1+q_j]} & \text{if } L(x) < L_m \text{ and } \frac{y}{x} \geq q_j \\ \frac{1}{[1+q_a]q_a^2}\left[\frac{y}{x}\right]^2 & \text{if } L(x) \geq L_m \text{ and } \frac{y}{x} < q_j \\ \frac{1}{[1+q_a]} & \text{if } L(x) \geq L_m \text{ and } \frac{y}{x} \geq q_j \end{cases}$
Irreversible mass	$\frac{dx_i}{dt} = \begin{cases} f(x_i,y_i)E_g(x_i,y_i,T) & \text{if } a_i > a_{hatch} \text{ and } E_g(x_i,y_i,T) > 0 \\ 0 & \text{otherwise} \end{cases}$
Reversible mass	$\frac{dy_i}{dt} = \begin{cases} [1-f(x_i,y_i)]E_g(x_i,y_i,T) & \text{if } a_i > a_{hatch} \text{ and } E_g(x_i,y_i,T) > 0 \\ E_g(x_i,y_i,T) & \text{if } a_i > a_{hatch} \text{ and } E_g(x_i,y_i,T) \leq 0 \\ 0 & \text{otherhwise} \end{cases}$

Herring cohort dynamics

Size-specific mortality	$\mu_{size}(x) = \mu_w \exp\left(-\frac{w(x)}{w_\mu}\right)$
Fisheries mortality	$\mu_{fish}(x) = \begin{cases} 0 & \text{if } l(x) < L_{fmin} \\ \mu_f\left[1+\exp\left(-\zeta_f\left[L(x)-L_{Hf}\right]\right)\right] & \text{if } l(x) \geq L_{fmin} \end{cases}$
Starvation mortality	$\mu_{starv}(x) = \begin{cases} \left[q_s\frac{x}{y}-1\right] & \text{if } y < q_s x \\ 0 & \text{if } y \geq q_s x \end{cases}$
Cohort density	$\frac{dN_i}{dt} = \begin{cases} -\mu_{el}N_i & \text{if } a_i < a_{hatch} \\ -\left[\mu_0+\mu_{size}(x_i)+\mu_{fish}(x_i)+\mu_{starv}(x_i,y_i)\right]N_i & \text{if } a_i \geq a_{hatch} \end{cases}$

2. Formulas for the instantaneous dynamics of the model at the start of the reproduction season ($(t = t_s \pmod{365})$)

Herring reproduction

Fecundity	$F_i = \begin{cases} \frac{k_r[y_i - q_r x_i]}{w(x_b)} & \text{if } \frac{y_i}{x_i} > q_r \\ 0 & \text{otherwise} \end{cases}$
Reversible mass	$y_i = \begin{cases} q_r x_i & \text{if } \frac{y_i}{x_i} > q_r \\ y_i & \text{otherwise} \end{cases}$
Total egg production	$F = \sum_i F_i$
Egg release in the environment	$N_{t+t_r}(t+t_r) = \begin{cases} \frac{F}{1+\exp\left(\frac{1}{2}\zeta_s\Delta_s\right)}\Phi_{SS}(T(t+t_r),E_{AF},E_{DF},T_{HF}) & \text{for } t_r = 0 \\ \left[\frac{F}{1+\exp\left(-\zeta_s\left[t_r-\frac{1}{2}\Delta_s\right]\right)} - \frac{F}{1+\exp\left(-\zeta_s\left[t_r-1-\frac{1}{2}\Delta_s\right]\right)}\right]\Phi_{SS}(T(t+t_r),E_{AF},E_{DF},T_{HF}) & \text{for } t_r = 1 \ldots \Delta_s - 1 \\ \left[F - \frac{F}{1+\exp\left(-\zeta_s\left[\frac{1}{2}\Delta_s - 1\right]\right)}\right]\Phi_{SS}(T(t+t_r),E_{AF},E_{DF},T_{HF}) & \text{for } t_r = \Delta_s \end{cases}$

Boundary condition of new cohorts

Egg period duration	$a_{hatch,i} = \epsilon_{min} + \Phi_{\mathrm{Arr}}(T,E_{AE})\epsilon_{egg} + \epsilon_{larv}$
Irreversible mass	$x_{t+t_r}(t+t_r) = x_b$
Reversible mass	$y_{t+t_r}(t+t_r) = q_j x_b$

1.2 Formulas cod-herring model

Tabel A2: Table with added formulas to describe cod dynamics.

Description	Equation
Representative weight cod	$w = \frac{m_{max} - m_{min}}{\ln(m_{max}) - \ln(m_{min})}$
Representative length cod	$l = \lambda_{1c} * w^{\lambda_{2c}}$
Arrhenius function	$\Phi_{Arr}(T, E_A) = \exp\left(-\frac{E_A}{k_B}\left(\frac{1}{T} - \frac{1}{T_r}\right)\right)$
Sharpe Schoolfield function	$\Phi_{SS}(T, E_A, E_D, T_H) = \frac{\exp\left(-\frac{E_A}{k_B}\left[\frac{1}{T} - \frac{1}{T_r}\right]\right)}{1 + \exp\left(-\frac{E_D}{k_B}\left[\frac{1}{T} - \frac{1}{T_H}\right]\right)}$
Biomass cod	
Biomass egg buffer cod	$\frac{dC_0}{dt} = (1 - k_3)\, v_3{}^+(T)C_3 \; + (1 - k_4)v_4{}^+(T)C_4 \; + v_5{}^+(T)C_5 - F_c C_0$
Biomass cod stage 1	$\frac{dC_1}{dt} = \; F_c C_0 + v_1(T)C_1 \; - \; \gamma_1{}^+(T)C_1 \; - \; \mu_1(T)C_1$
Biomass cod stage 2	$\frac{dC_2}{dt} = \; \gamma_1{}^+(T)C_1 \; + \; v_2(T)C_2 \; - \; \gamma_2{}^+(T)C_2 \; - \; \mu_2(T)C_2$
Biomass cod stage 3	$\frac{dC_3}{dt} = \; \gamma_2{}^+(T)C_2 \; + \; v_3(T)C_3 \; - \; (1 - k_3)\, v_3{}^+(T)C_3 \; - \; \gamma_3{}^+(T)C_3 \; - \; \mu_3(T)C_3$
Biomass cod stage 4	$\frac{dC_4}{dt} = \; \gamma_3{}^+(T)C_3 \; + \; v_4(T)C_4 \; - \; (1 - k_4)\, v_4{}^+(T)C_4 \; - \; \gamma_4{}^+(T)C_4 \; - \; \mu_4(T)C_4$
Biomass cod stage 5	$\frac{dC_5}{dt} = \; \gamma_4{}^+(T)C_4 \; + \; v_5(T)C_5 \; - \; v_5{}^+(T)C_5 \; - \; \mu_5(T)C_5$
Net biomass production cod	$v_j(T) \; = \; k_{ec} I_j(T) \; - \; E_j(T)$
Maintenance energy cod	$E_j(T) = \Phi_{Arr} \; \left(T, E_{AMC} + E_{iMC} \ln\left(\overline{w_j}\right)\right) \rho_{1c} \overline{w_j}^{\rho_{2c}}$
Transition rate change cod	$\gamma_j(T) = \frac{k_j v_j(T) - \mu_j}{1 - z_j{}^{1 - \mu_j / \left(k_j v_j(T)\right)}}$
Egg buff cod	$F_c = \begin{cases} \frac{\zeta_c \exp(-\zeta_c(\mathrm{t} - \mathrm{t_c} - 0.5\Delta_c))}{(1 + \exp(-\zeta_c(\mathrm{t} - \mathrm{t_c} - 0.5\Delta_c)))} R\Phi_{SS}(T, E_{AFC}, E_{DFC}, T_{HFC}) \text{ if } \mathrm{t} > \mathrm{t_c} \text{ and } \mathrm{t} < \mathrm{t_c} + \Delta_c \pmod{365} \\ 0 \text{ otherwise} \end{cases}$
Ingestion formulas cad	
Ingestion rate cod for certain prey	$I_{prey} = \frac{p_{prey}(l) a_{prey}(l) R_{prey}}{1 + h \sum_{prey} p_{prey}(l) a_{prey}(l) R_{prey}}$

Total ingestion of a certain cod stage

$$I_j = I_{zj} + I_{bj} + I_{blj} + I_{hj} + I_{cj}$$

Ingestion of zooplankton by cod stage *j*

$$I_{zj}(T) = \frac{p_{zj}a_{zj}(T)R_z}{1 + h_j(T)\left[p_{zj}a_{zj}(T)R_z + p_{bj}a_{bj}(T)R_b + p_{blj}a_{blj}(T)R_{bl} + \sum_k p_{fj}s_{kj}a_{fj}(T)C_k + \sum_i s_{ij}p_{fj}a_{hj}(T)N_i w(x_i)\right]}$$

Ingestion of small benthos by cod stage *j*

$$I_{bj}(T) = \frac{p_{bj}a_{bj}(T)R_b}{1 + h_j(T)\left[p_{zj}a_{zj}(T)R_z + p_{bj}a_{bj}(T)R_b + p_{blj}a_{blj}(T)R_{bl} + \sum_k p_{fj}s_{kj}a_{fj}(T)C_k + \sum_i s_{ij}p_{fj}a_{jf}(T)N_i w(x_i)\right]}$$

Ingestion of large benthos by cod stage *j*

$$I_{blj}(T) = \frac{p_{blj}a_{blj}(T)R_{bl}}{1 + h_j(T)\left[p_{zj}a_{zj}(T)R_z + p_{bj}a_{bj}(T)R_b + p_{blj}a_{blj}(T)R_{bl} + \sum_k p_{fj}s_{kj}a_{fj}(T)C_k + \sum_i s_{ij}p_{fj}a_{fj}(T)N_i w(x_i)\right]}$$

Ingestion of herring in cohort *i* by cod stage *j*

$$I_{ij}(T) = \frac{p_{fj}s_{ij}a_{fj}(T)N_i}{1 + h_j(T)\left[p_{zj}a_{zj}(T)R_z + p_{bj}a_{bj}(T)R_b + p_{blj}a_{blj}(T)R_{bl} + \sum_k p_{fj}s_{kj}a_{fj}(T)C_k + \sum_i s_{ij}p_{fj}a_{fj}(T)N_i w(x_i)\right]}$$

Ingestion of cod in stage *k* by cod stage *j*

$$I_{kj}(T) = \frac{p_{fj}s_{kj}a_{fj}(T)C_k}{1 + h_j(T)\left[p_{zj}a_{zj}(T)R_z + p_{bj}a_{bj}(T)R_b + p_{blj}a_{blj}(T)R_{bl} + \sum_k p_{fj}s_{kj}a_{fj}(T)C_k + \sum_i s_{ij}p_{fj}a_{fj}(T)N_i w(x_i)\right]}$$

Total herring ingestion by cod stage *j*

$$I_{hj}(x,T) = \sum_i I_{ij}(T)\, w(x_i)$$

Total cod ingestion by cod stage *j*

$$I_{cj}(x,T) = \sum_k I_{kj}(T)$$

Preference for prey formulas

Relative preference for a certain prey type

$$p_{prey}(l) = \frac{p_{prey}(l)}{\sum_{prey} p_{prey}(l)}$$

Preference for zooplankton by cod

$$p_z(l) = s_{1z}e^{-s_{2z}l}$$

Preference for small benthos by cod

$$p_b(l) = s_{minb} + \frac{s_{maxb} - s_{minb}}{1 + e^{-\zeta_b*(L-L_{Hb})}}$$

Preference for large benthos by cod	$p_{bl}(l) = \begin{cases} 0, l < l_{minbl} \\ \frac{s_{maxbl}}{1 + e^{-\zeta_{bl}*(L-L_{Hbl})}} \end{cases}$
Preference for fish by cod	$p_f(l) = \begin{cases} 0, l < l_{minf} \\ \frac{s_{maxf}}{1 + e^{-\zeta_{f}*(L-L_{Hf})}} \end{cases}$
Diet adjusting formula	$\begin{cases} 0 & if\ l_{sj}\ and\ l_{fj} < 15 \\ p_{prey}(l) = \frac{p_{prey}(l)}{\sum_{prey} p_{prey}(l)} & otherwise \end{cases}$
Consumption size preference for herring by cod	$s_{ij} = \begin{cases} \frac{l_i - \Omega_{min}\overline{l_j}}{(\Omega_{opt} - \Omega_{min})\overline{l_j}} \text{ if } \Omega_{min}\overline{l_j} < l_i < \Omega_{opt}\overline{l_j} \\ \frac{\Omega_{max}\overline{l_j} - l_i}{(\Omega_{max} - \Omega_{opt})\overline{l_j}} \text{ if } \Omega_{opt}\overline{l_j} < l_i < \Omega_{max}\overline{l_j} \\ 0 \text{ otherwise} \end{cases}$
Consumption size preference for cod by cod	$s_{kj} = \begin{cases} \frac{\overline{l_k} - \Omega_{min}\overline{l_j}}{(\Omega_{opt} - \Omega_{min})\overline{l_j}} \ if\ \Omega_{min}\overline{l_j} < \overline{l_k} < \Omega_{opt}\overline{l_j} \\ \frac{\Omega_{max}\overline{l_j} - \overline{l_k}}{(\Omega_{max} - \Omega_{opt})\overline{l_j}} \ if\ \Omega_{opt}\overline{l_j} < \overline{l_k} < \Omega_{max}\overline{l_j} \\ 0\ otherwise \end{cases}$
Handling time and attack rate	
Handling time cod	$h_j(T) = \frac{d_{1c}\overline{w_j}^{d_{2c}}}{\Phi_{SS}(T, E_{AHC}, E_{DHC}, T_{HHC})}$
Attack rate zooplankton by cod	$a_{zj}(T) = \Phi_{Arr}\left(T, E_{AM} + E_{iM}\ln(\overline{w_j})\right) A_{maxc}\left[\frac{\overline{w_j}}{w_{optc}}\exp\left(1 - \frac{\overline{w_j}}{w_{optc}}\right)\right]^{\alpha_c}$
Attack rate small benthos by cod	$a_{bj}(T) = \Phi_{Arr}\left(T, E_{AM} + E_{iM}\ln(\overline{w_j})\right) b_{1cb}\overline{w_j}^{b_{2cb}}$
Attack rate large benthos by cod	$a_{blj}(T) = \Phi_{Arr}\left(T, E_{AM} + E_{iM}\ln(\overline{w_j})\right) b_{1cbl}\overline{w_j}^{b_{2cbl}}$
Attack rate fish by cod	$a_{fj}(T) = \Phi_{Arr}\left(T, E_{AM} + E_{iM}\ln(\overline{w_j})\right) b_{1cf}\overline{w_j}^{b_{2cf}}$
Mortality cod	
Total mortality of cod	$\mu_j = \mu_0 + \mu_{sizej} + \mu_{fishj} + \mu_{canj}$
Size specific background	$\mu_{sizej} = \mu_{wc}\exp(-\frac{\overline{l_j}}{l_{\mu c}})$

mortality of cod	
Size specific fishing mortality	$\mu_{fishj} = \begin{cases} 0 & if\ l(x) < L_{fminc} \\ \dfrac{\mu_{fc}}{1+\exp(-\zeta_{fc}(\mathrm{L_j} - \mathrm{L}_{Hfc}))} & if\ l(x) \geq L_{fminc} \end{cases}$
Starvation mortality due to cannibalism	$\mu_{canj} = \sum_k I_{kj}(T)$
Prey dynamics	
Zooplanton	$\frac{dR_z}{dt} = \Phi_{SS}(T, E_{AP}, E_{DP}, T_{HP})\left[\Gamma - \frac{1-\Gamma}{1+\exp(-\zeta_l(Q-Q_H))}\right]P_z - \Phi_{Arr}(T, E_{AR})\, r_z R_z - \sum_i I_z(T)\ N_i - \sum_j I_{zj}(T) C_j$
Small benthos	$\frac{dR_b}{dt} = \Phi_{SS}(T, E_{AP}, E_{DP}, T_{HP})\, P_b - \Phi_{Arr}(T, E_{AR})\, r_b R_b - \sum_i I_b(T)\ N_i - \sum_j I_{bj}(T) C_j$
Large benthos	$\frac{dR_{bl}}{dt} = \Phi_{SS}(T, E_{AP}, E_{DP}, T_{HP})\, P_{bl} - \Phi_{Arr}(T, E_{AR})\, r_{bl} R_{bl} - \sum_j I_{blj}(T) C_j$
Adjusted herring formula	
Total herring mortality	$\frac{dN_i}{dt} = \begin{cases} -\mu_{size} N_i & if\ a_i < 0 \\ -[\mu_0 + \mu_{size}(x) + \mu_{fish}(x) + \mu_{starv}(x,y)]N_i - \sum_j I_{ij} C_i & if\ a_i \geq 0 \end{cases}$

1.3 Graphs parametrisation

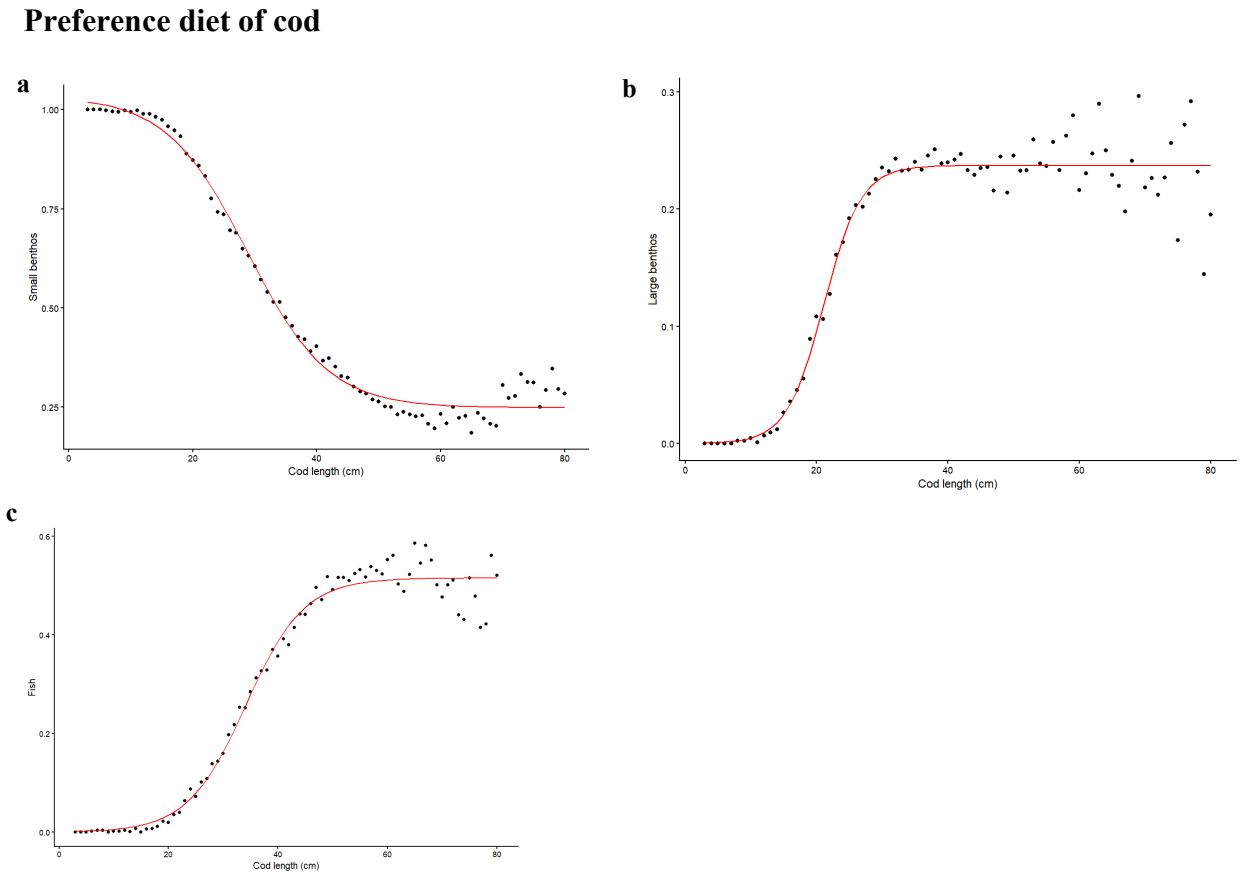


Figure A9: Fitted functions (line) for cod preference for small benthos (a), large benthos (b) and fish (c) to stomach data (points) from Lindmark et al. (2025). The functions are described in equations 26-28.

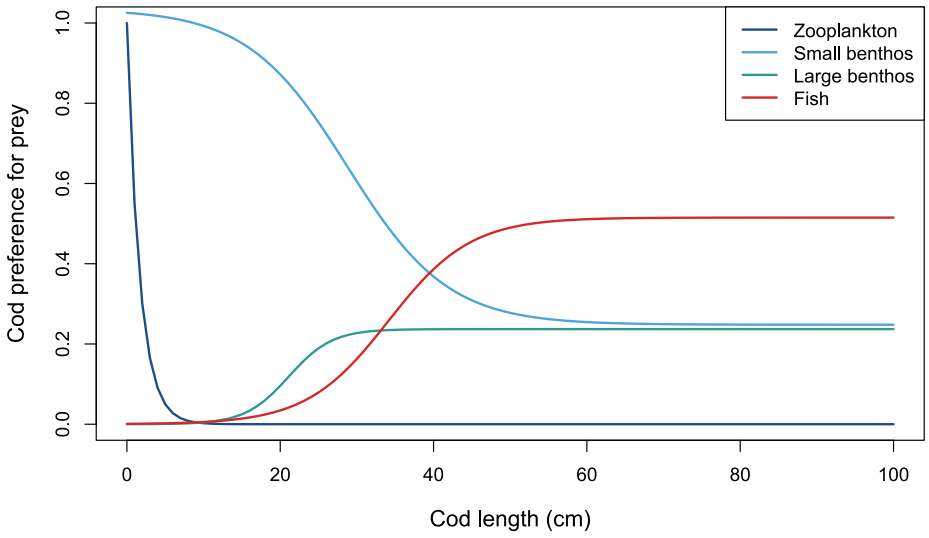


Figure A10: Preferences for each resource as a function of cod length.

Table A3: Preference values of the different cod stages for the different resources. Column represents the prey types, and the rows represents the cod stages.

P_{z1}	0.0147	P_{b1}	0.9853	P_{bl1}	0.0000	P_{f1}	0.0000
P_{z2}	0.0000	P_{b2}	0.8170	P_{bl2}	0.1353	P_{f2}	0.0477
P_{z3}	0.0000	P_{b3}	0.3415	P_{bl3}	0.2378	P_{f3}	0.4207
P_{z4}	0.0000	P_{b4}	0.2484	P_{bl4}	0.2369	P_{f4}	0.5147
P_{z5}	0.0000	P_{b5}	0.2480	P_{bl5}	0.2370	P_{f5}	0.5150

Prey-predator size ratio

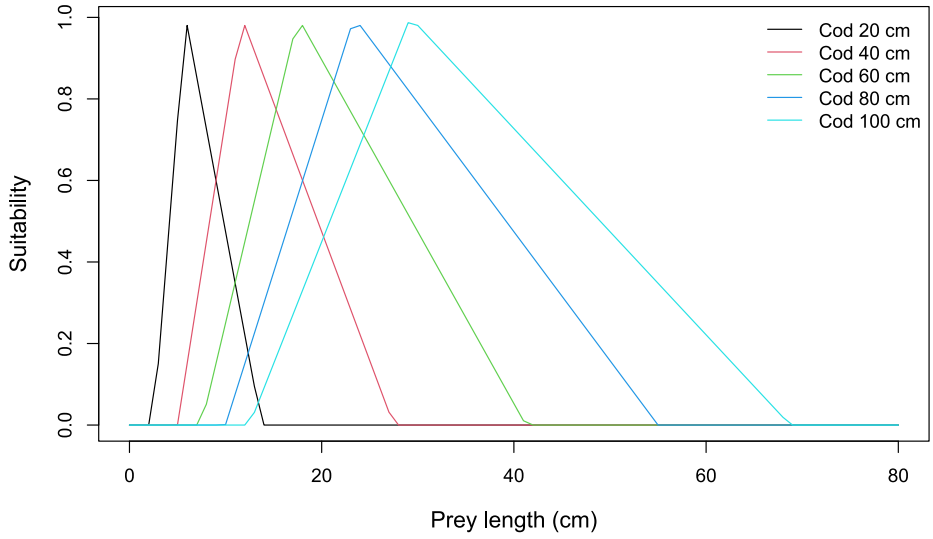


Figure A3: Predator-prey length suitability for different cod sizes, based on the data from Kulatska et al. (2019).

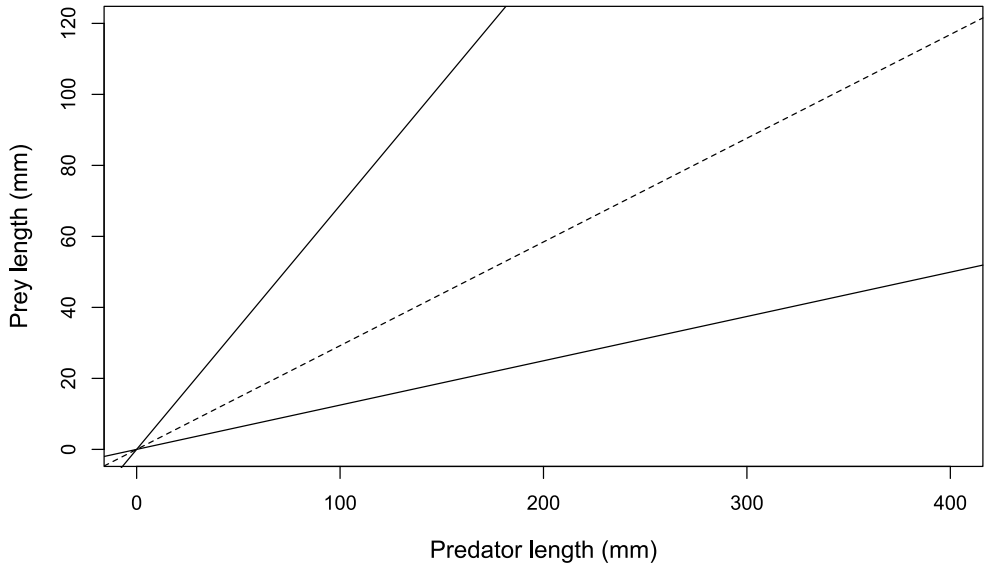


Figure A4: Prey length as a function of predator length. The dotted line represents the optimal prey length, while the solid lines represent the minimum and maximum prey lengths for a given predator length.

Table A4: Abstracted values for minimum/optimum/maximum size from graph Kulatska et al. (2019) for different cod sizes. From these values the mean was taken as the parameter value in my model.

Cod size (cm)	20	40	60	80	100	mean
Minimum size (cm)	-	0,125	0,117	0,138	0,120	0,125
Optimum size (cm)	0,300	0,300	0,283	0,288	0,290	0,292
Maximum size (cm)	0,700	0,675	-	-	-	0,688

Cod growth

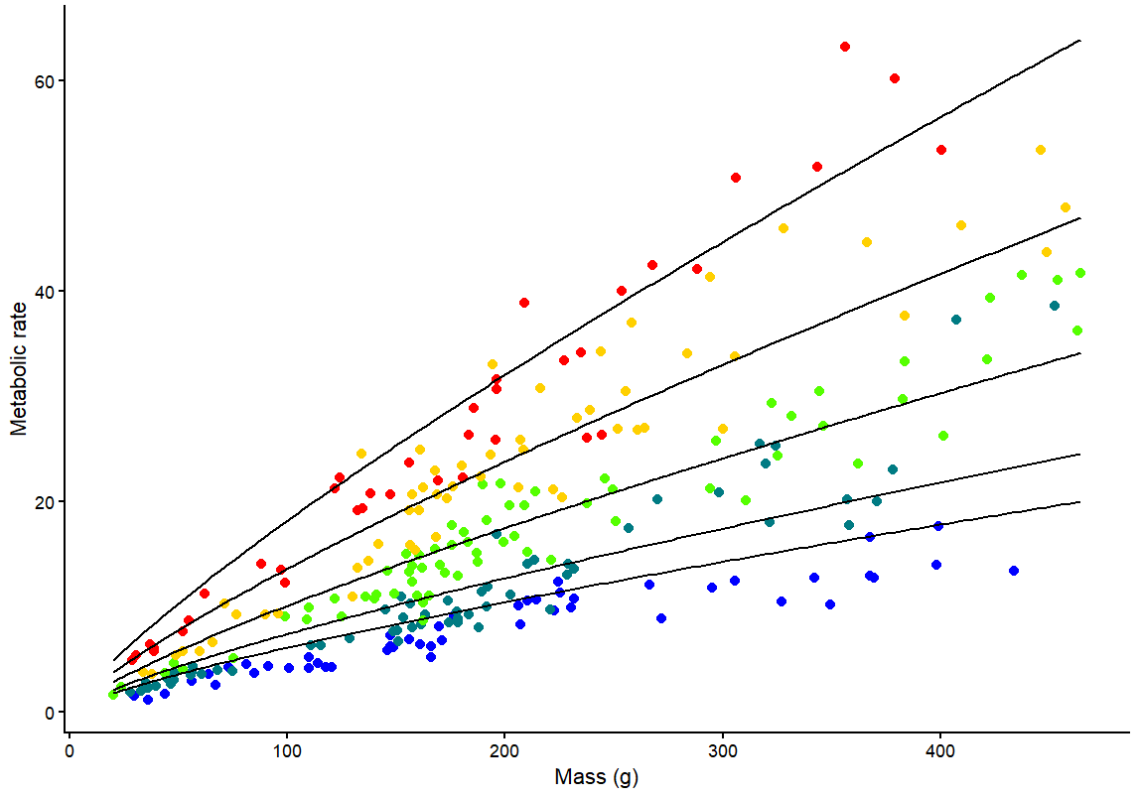


Figure A5: Metabolic rate (mg O2/h) of cod in function of mass of cod (g) for temperatures 2 °C (blue), 5 °C (blue green), 10 °C (green), 15 °C (orange), 20 °C (red). These results are used for obtaining parameter values for the maintenance costs in the model.

Handling time cod

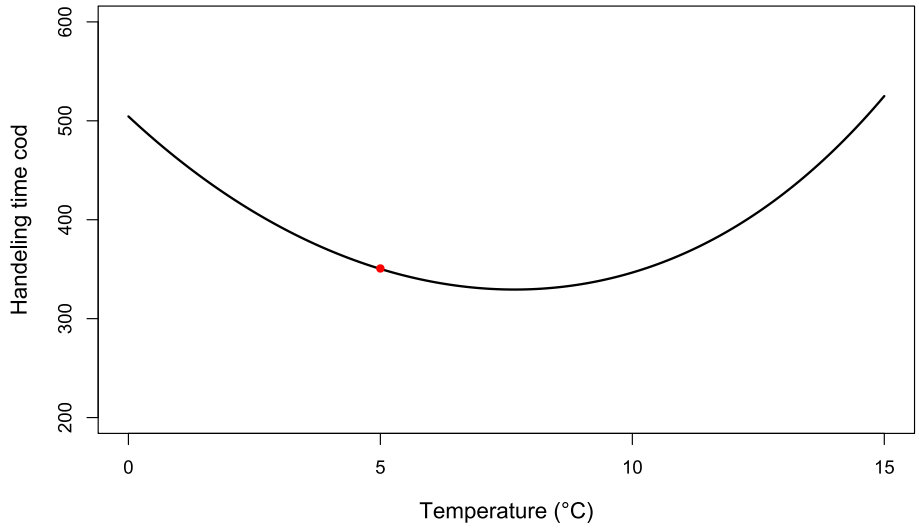


Figure A6: The red dot is the calculated point out of the parameter values used in van Leeuwen et al. (2013) of the temperature-dependent handling time for a cod of 10 cm length. The black line is the fitted curve for the temperature center, which is 8.588 °C, this is the temperature used in the model without any warming.

Mortality

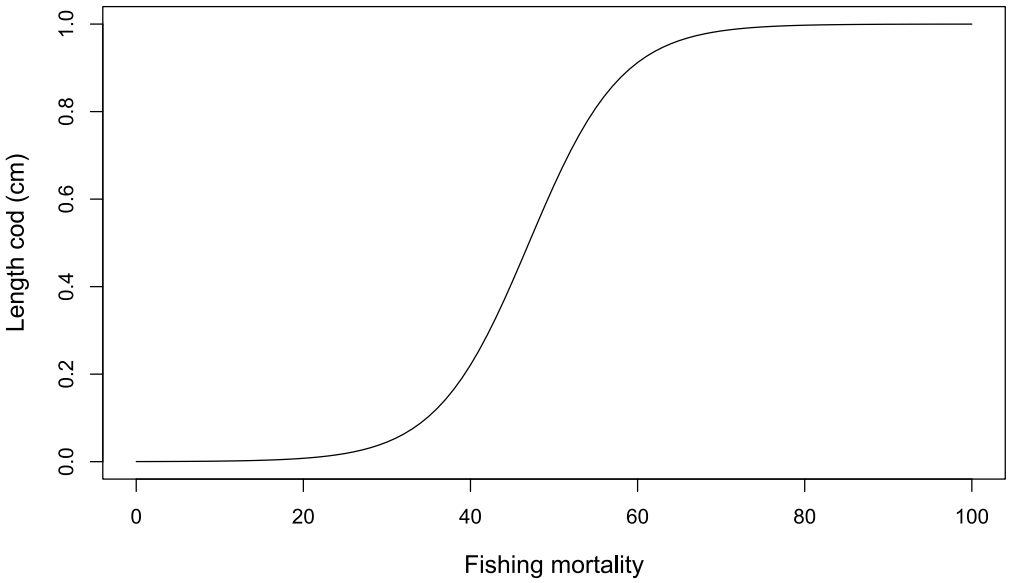


Figure A7: Fishing mortality in function of cod length (cm).

1.4 Parameter values herring model

Table A5: Parameter values used for model calculations herring model (Table reproduced from Croll et al. submitted).

Temperature and light			
T_c	Temperature center	8.588	°C
a_c	Temperature amplitude center	7.69	°C
a_a	Temperature amplitude amplitude	5.914	°C
a_s	Temperature amplitude shift	273.1	days
s_c	Temperature shift center	172.1	days
s_a	Temperature shift amplitude	47.06	days
s_s	Temperature shift shift	4.6	days
Q_c	Light center	0.5	-
Q_a	Light amplitude	0.5	-
Q_s	Light shift	173	days
Prey communities			
P_z	Zooplankton productivity	0.25	g day^{-1}
P_b	Zoobenthos productivity	0.5	g day^{-1}
r_z	Zooplankton turnover rate	0.1	day^{-1}
r_b	Zoobenthos turnover rate	0.01	day^{-1}
Γ	Zooplankton productivity fraction without light	0.1	-
ζ_l	Zooplankton light sensitivity slope scaler	50	-
Q_H	Light condition at half the maximum zooplankton productivity	0.403	-
E_{AP}	Activation energy prey productivity	1.504	eV
E_{DP}	Deactivation energy prey productivity	3.861	eV
T_{HP}	Temperature at half deactivation of prey productivity	25.01	°C
E_{AR}	Activation energy prey turnover rate	0.8178	eV
Herring weight conversion			
λ_1	Allometric scaler	5.65	cm $g^{-\lambda_2}$
λ_2	Allometric exponent	0.32	-
Herring development			
x_b	Structural mass at first feeding	0.0007	g
L_m	Size at maturation	14	cm
ϵ_{min}	Minimum duration of the egg period	4.23	days
ϵ_{egg}	Egg-larvae period scaler	9.08	days
ϵ_{larv}	Minimum duration non-feeding larval period	25	days
q_j	Juvenile asymptotic condition	3.09	-
q_a	Adult asymptotic condition	5	-
q_r	Minimal condition for reproduction	0.7	-
q_s	Starvation threshold	0.2	-

E_{AE}	Activation energy duration egg-larval period	-0.5029	eV
Herring consumption			
A_{max}	Maximum zooplankton attack rate	150	$m^3 day^{-1}$
w_{opt}	Optimum zooplankton consumption size	50	g
α	Allometric exponent zooplankton attack rate	0.5	-
b_1	Allometric scaler zoobenthic attack rate	0.2	$m^2 g^{b_2} day^{-1}$
b_2	Allometric exponent zoobenthic attack rate	-	-
d_1	Allometric scaler digestion	4.8	$day\ g^{-1-b_2}$
d_2	Allometric exponent digestion	-0.74	-
B_{max}	Maximum preference for zoobenthos	0.4	-
ζ_B	Feeding switch slope scaler	1.5	-
L_{HB}	Size at half the maximum zoobenthos preference	20	cm
E_{AH}	Activation energy digestion	0.5446	eV
E_{DH}	Deactivation energy digestion	5.142	eV
T_{HH}	Temperature at half deactivation digestion	24.09	°C
Herring energetics			
ρ_1	Allometric scaler metabolism	0.03	$g^{1-\lambda_2} day^{-1}$
ρ_2	Allometric exponent metabolism	0.8	-
k_e	Energy conversion efficiency	0.5	-
E_{AM}	Activation energy metabolic rate	0.62	eV
E_{iM}	Size-specific activation energy metabolic rate	0.018	$eV - \ln(g)$
Herring mortality			
μ_w	Weight specific mortality constant	0.01	day^{-1}
w_μ	Weight specific mortality scaler	0.5	g
μ_f	Fishing mortality scaler	varied	day^{-1}
ζ_f	Size slope scaler for fishing mortality	0.96	-
L_{fmin}	Minimum target size of fisheries	5.6	cm
L_{Hf}	Length at half maximum fishing mortality	8	cm
μ_0	Background mortality	0.002	day^{-1}
μ_{el}	Egg and larvae mortality	0.03	day^{-1}
E_{AF}	Activation energy egg survival	-0.5029	eV
E_{DF}	Deactivation energy egg survival	-8.8534	eV
T_{HF}	Temperature at half deactivation egg survival	4.5019	°C
Reproduction			
k_r	Gonad conversion efficiency	0.5	-
ζ_s	Egg release slope scalar	1	day
Δ_S	Duration of the spawning	76	days
t_s	First day of spawning season	varied	Julian date

1.5 Parameter values cod-herring model

Tabel A6: Parameter values used for model calculations cod-herring model.

Length-limits cod stages				
l_{1min}	Minimum length in cod stage 1	0.39	cm	Finn et al. 2002
l_{1max}	Maximum length in cod stage 1	15	cm	Lindmark et al. 2025
l_{2min}	Minimum length in cod stage 2	15	cm	Lindmark et al. 2025
l_{2max}	Maximum length in cod stage 2	30	cm	Vainikka et al. 2009
l_{3min}	Minimum length in cod stage 3	30	cm	Vainikka et al. 2009
l_{3max}	Maximum length in cod stage 3	55	cm	Chosen intermediate value
l_{4min}	Minimum length in cod stage 4	55	cm	Chosen intermediate value
l_{4max}	Maximum length in cod stage 4	100	cm	Lindmark et al. 2025
l_{5min}	Minimum length in cod stage 5	100	cm	Lindmark et al. 2025
l_{5max}	Maximum length in cod stage 5	100	cm	Lindmark et al. 2025
λ_{1c}	Length weight scaler for cod	4.64	cm $g^{-\lambda_2}$	Coull et al. 1989
λ_{2c}	Length weight exponent for cod	0.33	-	Coull et al. 1989
Preferences diet				
s_{1z}	Preference scaler for zooplankton	1	-	Lindmark et al. 2025
s_{2z}	Preference exponent for zooplankton	0.60	-	Lindmark et al. 2025
s_{minb}	Minimum preference constant for small zoobenthic invertebrates	1.035	-	Lindmark et al. 2025
s_{maxb}	Maximum preference constant for small zoobenthic invertebrates	0.248	-	Lindmark et al. 2025
ζ_b	Slope of preference curve for small zoobenthic invertebrates	0.153	cm^{-1}	Lindmark et al. 2025

L_{Hb}	Predator size at which the preference is half of s_{maxb}	28.781	cm	Lindmark et al. 2025
s_{maxbl}	Maximum preference constant for large zoobenthic invertebrates	0.237	-	Lindmark et al. 2025
ζ_{bl}	Slope of preference curve for large zoobenthic invertebrates	0.353	cm^{-1}	Lindmark et al. 2025
L_{Hbl}	Predator size at which the preference is half of s_{maxbl}	21.096	cm	Lindmark et al. 2025
l_{minbl}	Minimum length of cod for eating large zoobenthic invertebrates	15	cm	Lindmark et al. 2025
s_{maxf}	Maximum preference constant for fish	0.515	-	Lindmark et al. 2025
ζ_f	Slope of preference curve for fish	0.187	cm^{-1}	Lindmark et al. 2025
L_{Hf}	Predator size at which the preference is half of s_{maxf}	34.12	cm	Lindmark et al. 2025
l_{minf}	Minimum length of cod for eating fish	15	cm	Lindmark et al. 2025
Attack rates				
A_{maxc}	Cod maximum zooplankton attack rate	9	day^{-1}	Byström & García-Berthou 1999
w_{optc}	Cod optimal weight for attack on zooplankton	4.7	g	Byström & García-Berthou 1999
α_c	Cod zooplankton attack rate scaler	0.62	-	Byström & García-Berthou 1999
b_{1cb}	Cod Allometric scaler small benthos attack rate	0.4	$days/g^{(1+d2c)}$	van Leeuwen et al. 2014
b_{2cb}	Cod Allometric exponent small benthos attack rate	0.6	-	van Leeuwen et al. 2014
b_{1cbl}	Cod Allometric scaler large benthos attack rate	0.4	$days/g^{(1+d2c)}$	van Leeuwen et al. 2014
b_{2cbl}	Cod Allometric exponent large benthos attack rate	0.6	-	van Leeuwen et al. 2014
b_{1cf}	Cod Allometric scaler fish attack rate	1.6	$days/g^{(1+d2c)}$	Claessen et al. 2000

b_{2cf}	Cod Allometric exponent fish attack rate	0.6	-	Claessen et al. 2000
Prey-predator size ratio				
Ω_{min}	Minimum fish prey/predator length ratio	0.125	-	Kulatska et al. 2019
Ω_{opt}	Optimal fish prey/predator ratio	0.292	-	Kulatska et al. 2019
Ω_{max}	Maximum fish prey/predator ratio	0.688	-	Kulatska et al. 2019
Cod body growth				
k_{ec}	Assimilation efficiency of cod	0.6	-	Peters 1983
k_3	Fraction of net production that is invested in somatic growth in cod	0.8	-	Own reasoning
k_4	Fraction of net production that is invested in somatic growth in cod	0.4	-	Own reasoning
E_{AMC}	Activation energy metabolic rate	0.339	eV	Lindmark et al. 2022
E_{iMC}	Length specific activation energy for metabolic rate	0.018	eV	Lindmark et al. 2022
ρ_{1c}	Allometric scaler metabolism	0.0147	$\text{days/g}^{(1-\rho 2c)}$	Lindmark et al. 2022
ρ_{2c}	Allometric exponent metabolism	0.791	-	Lindmark et al. 2022
Handling time				
d_{1c}	Allometric scaler handling time	190.1	$\text{days/g}^{(1+d2c)}$	Björnsson et al. 2007
d_{2c}	Allometric exponent handling time	-2.34	-	Björnsson et al. 2007
E_{AHC}	Activation energy handling time cod	0.73	eV	Lindmark et al. 2022
E_{DHC}	Deactivation energy handling time cod	1.89	eV	Lindmark et al. 2022
T_{HHC}	Temperature of half deactivation of handling time cod	9.34	°C	Lindmark et al. 2022
Reproduction and egg survival				
ζ_c	Reproduction biomass release rate for cod	1	g day^{-1}	Assumed value
t_c	Starting day of the year for cod reproduction	152	days	Bleil et al. 2009

Δ_c	Duration of the cod reproductive season	121	days	Bleil et al. 2009
E_{AFC}	Activation energy cod egg survival	-3.5	Ev	Peck et al. 2012
E_{DFC}	Deactivation energy cod egg survival	-7	Ev	Peck et al. 2012
T_{HFC}	Temperature at half deactivation cod egg survival	5	℃	Peck et al. 2012
R	Egg survival constant	0.311	-	Peck et al. 2012
Productivity benthos				
P_{bl}	Productivity of large benthos	0.005	g day^{-1}	Varied value of Croll et al. submitted
r_{bl}	Large benthos turnover rate	0.01	day^{-1}	Varied value Claessen et al. 2000
Mortality				
μ_{fc}	Maximum fishing pressure on cod	0.0001	day^{-1}	Varied value
ζ_{fc}	Fisheries slope scaler cod	0.173	cm^{-1}	Kvamme & Isaksen 2004
L_{Hfc}	Length at half the maximum fishing pressure for cod	49.21	cm	Kvamme & Isaksen 2004
L_{fminc}	Minimum fished length cod	15	cm	Kvamme & Isaksen 2004
μ_{wc}	Max cod size specific mortality rate	0.03	day^{-1}	Croll et al. submitted
$w_{\mu c}$	Cod size specific mortality rate scaler	0.5	g	Croll et al. submitted
μ_{0c}	Background mortality rate cod	0.0005	day^{-1}	Varied value

2. Results

Temperature bifurcation herring (non-log)

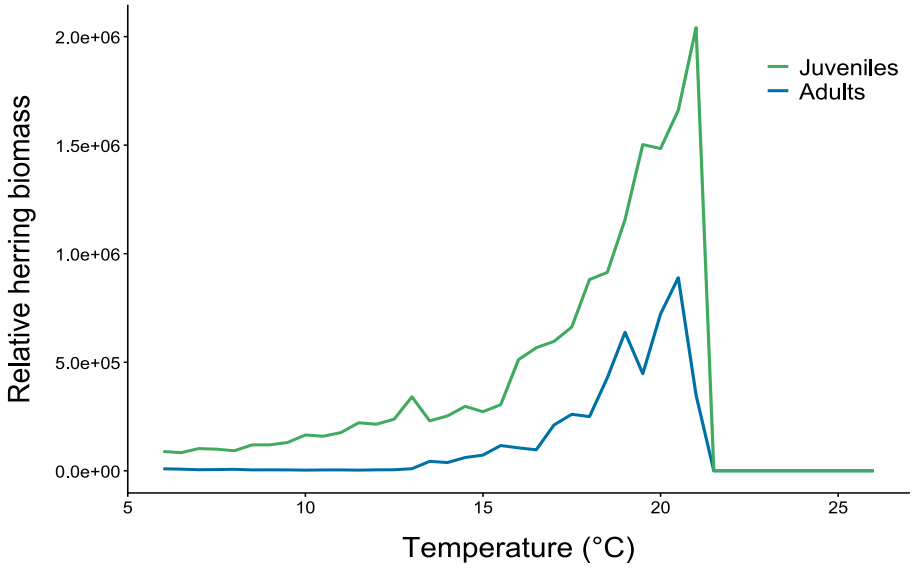


Figure A8: Bifurcation graphs of herring biomass density (on a non-log scale) varying with temperature. The bifurcations are made between 6 and 26 °C, the used step size is 0.5 °C and the output is generated every year at the start of the reproduction period. The full line represents the average biomass in each year of the period of the population cycle.

Cod biomass at 8 °C and 12 °C

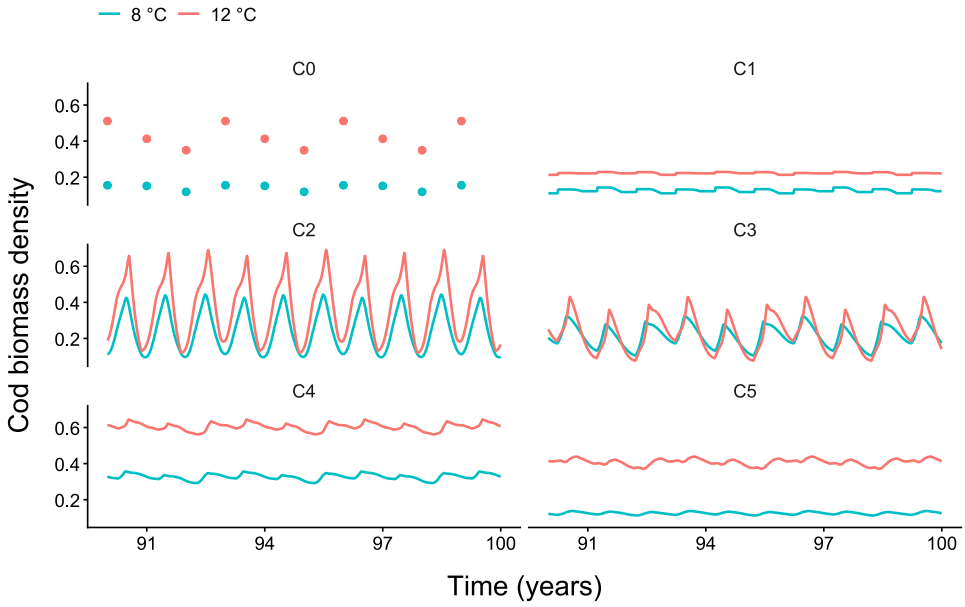


Figure A9: Cod biomass density (non-log) across time (year) for each cod stage (C1, C2, C3, C4, C5) and the number of eggs at the beginning of the reproduction period (C0), at 8 °C and 12 °C.

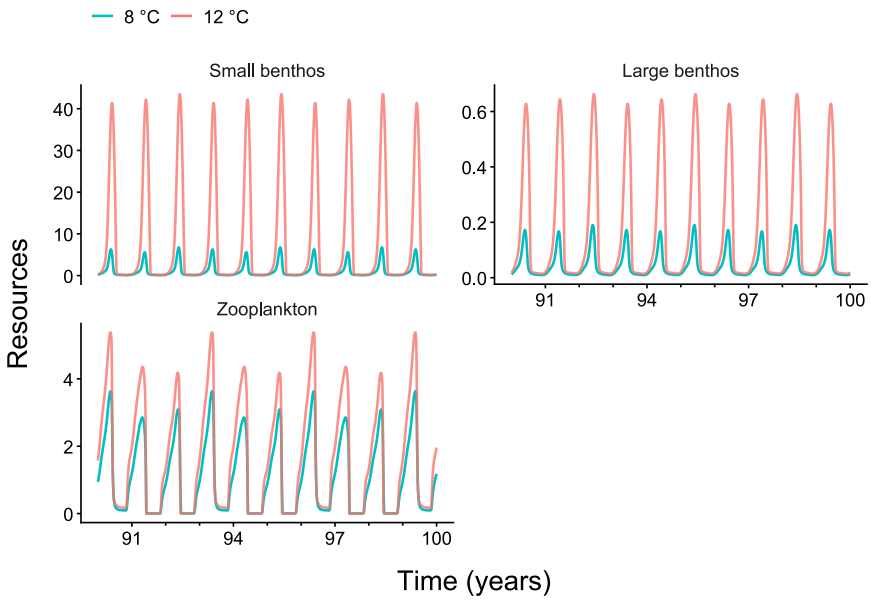


Figure A10: Densities (non-log) of small benthos, large benthos and zooplankton across time (years) at 8 °C compared to 12 °C.

Cod dynamics at 12°C and 15 °C

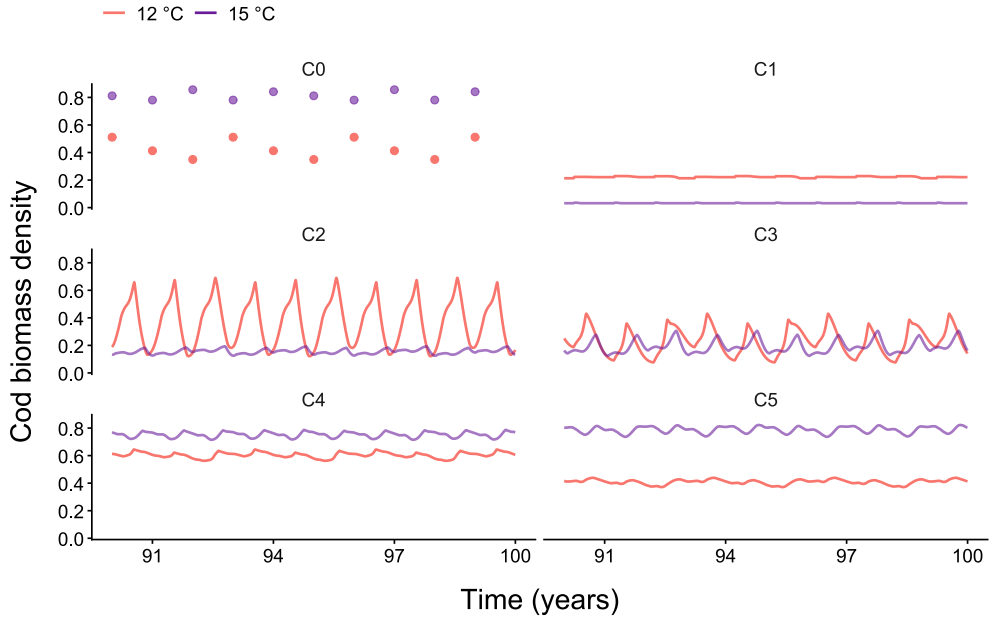


Figure A11: Cod biomass density (non-log) across time (year) for each cod stage (C1, C2, C3, C4, C5) and the number of eggs at the beginning of the reproduction period (C0), at 12 °C and 15 °C.

Egg survival cod

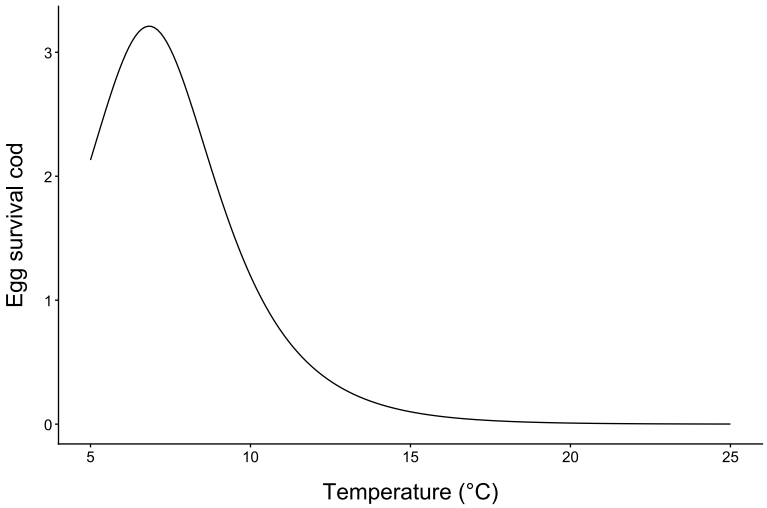


Figure A12: Egg survival of cod as a function of temperature (°C).

Resource densities at 12 °C and 15 °C

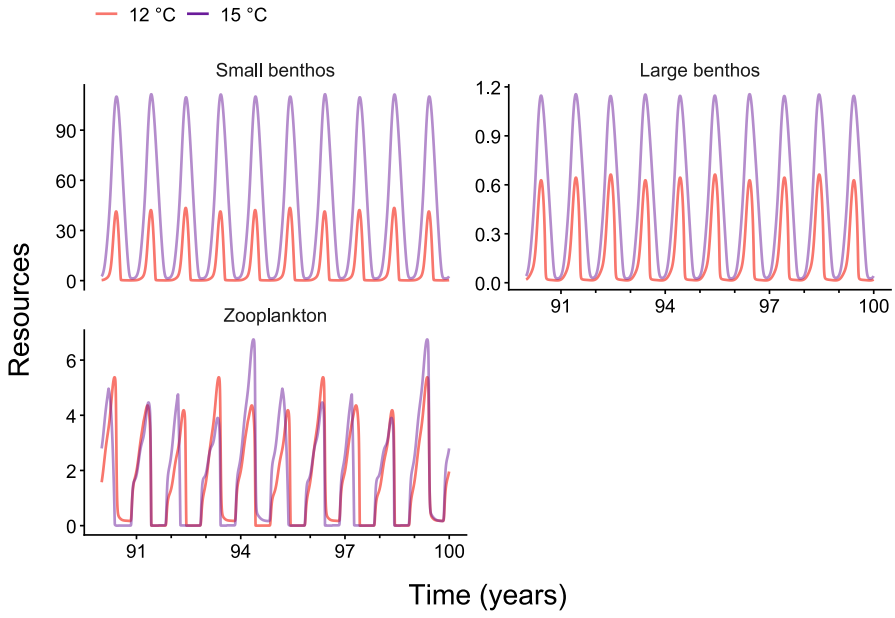


Figure A13: Densities (non-log) of small benthos, large benthos and zooplankton across time (years) at 12 °C compared to 15 °C.

Stage durations cod

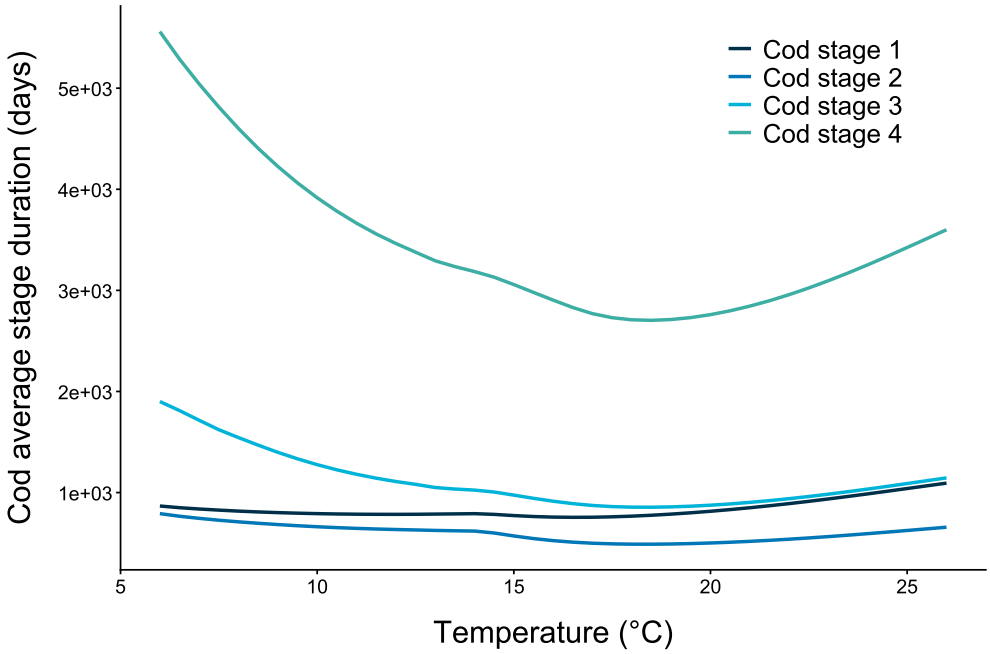


Figure A14: Average stage duration (days) of the different cod stages varying with temperature (°C) on a non-log scale.

Herring biomass at 8 °C and 12 °C (non-log)

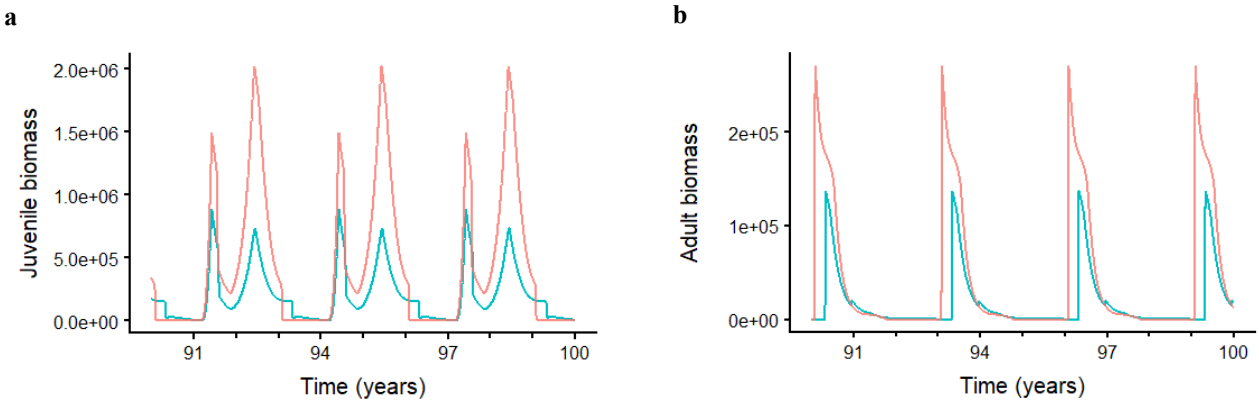


Figure A15: Variation in juvenile biomass (log) (b) and adult biomass (log) (c) herring across time (years), at 8 °C and 12 °C.

Herring biomass at 12 °C and 15 °C

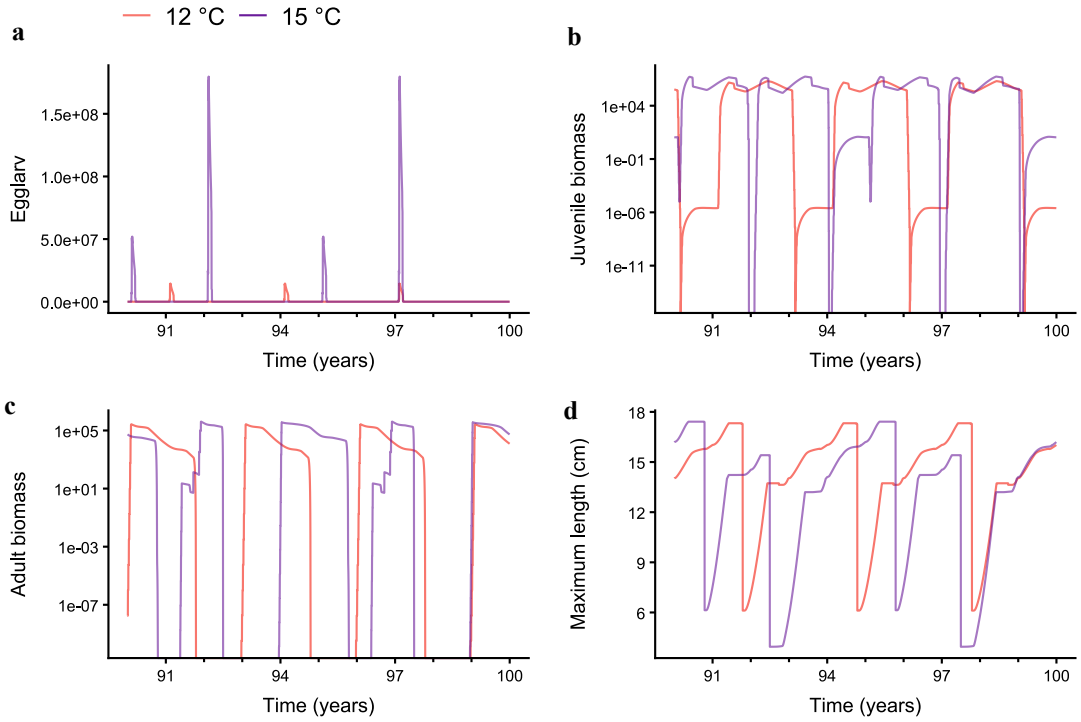
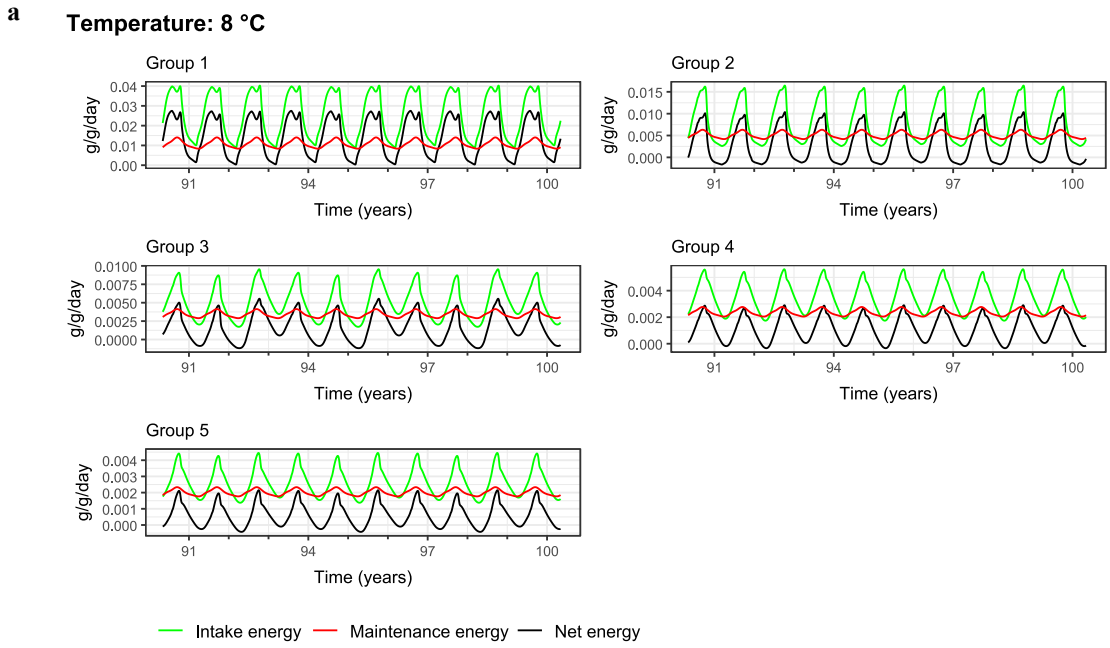
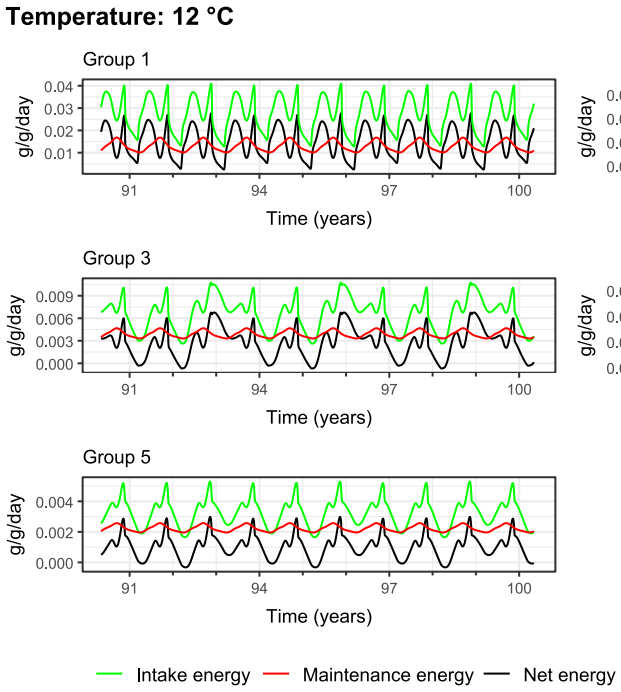


Figure A16: Variation in Egglarv (total amount of released eggs and larvae) (non-log) (a), juvenile biomass (log) (b), adult biomass (log) (c), and maximum length (non-log) (d) of herring across time (years), at 12 °C and 15 °C.

Graphs maintenance energy



b



c

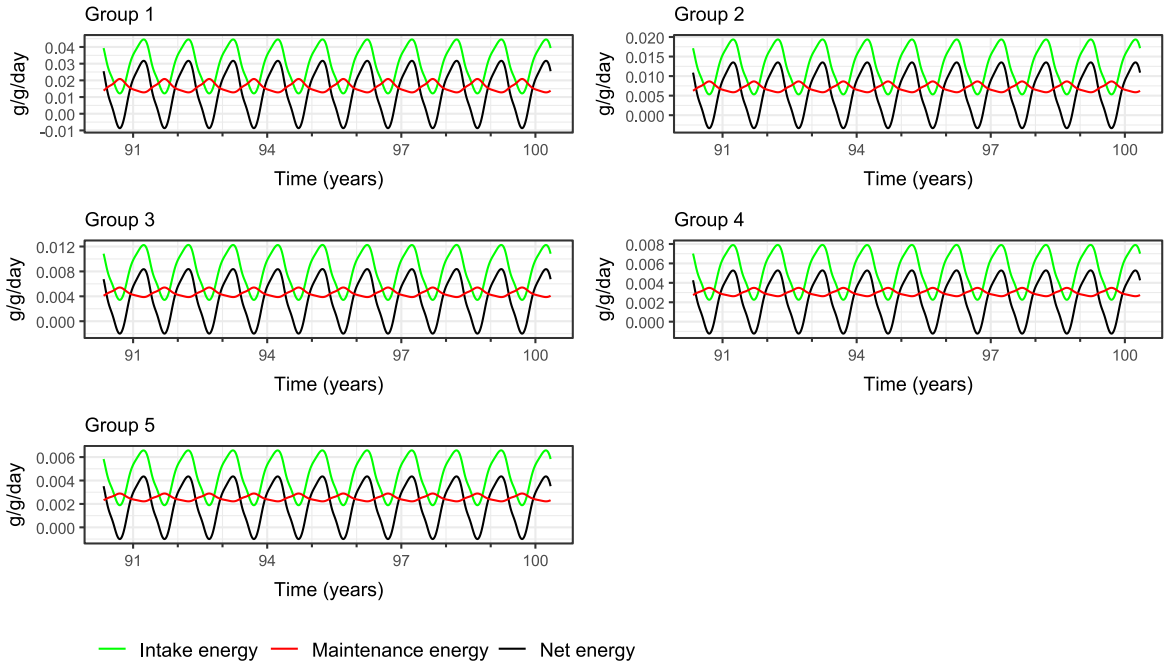


Figure A17: Intake energy, maintenance energy, net energy gain across time (years), at temperatures 8 °C (a), 12 °C (b) and 17 °C (c).

Handling time for cod

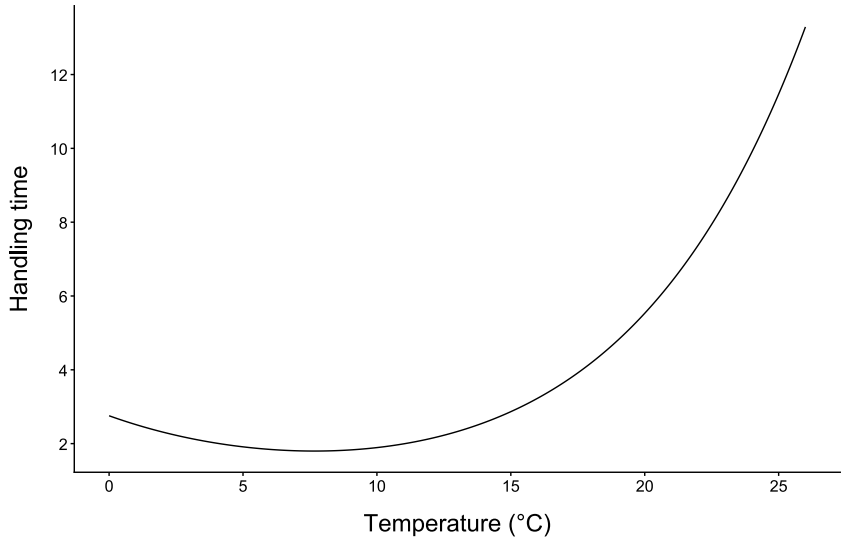


Figure A18: Handling time for cod as a function of temperature (°C).

Herring biomass at 16 °C and 17 °C

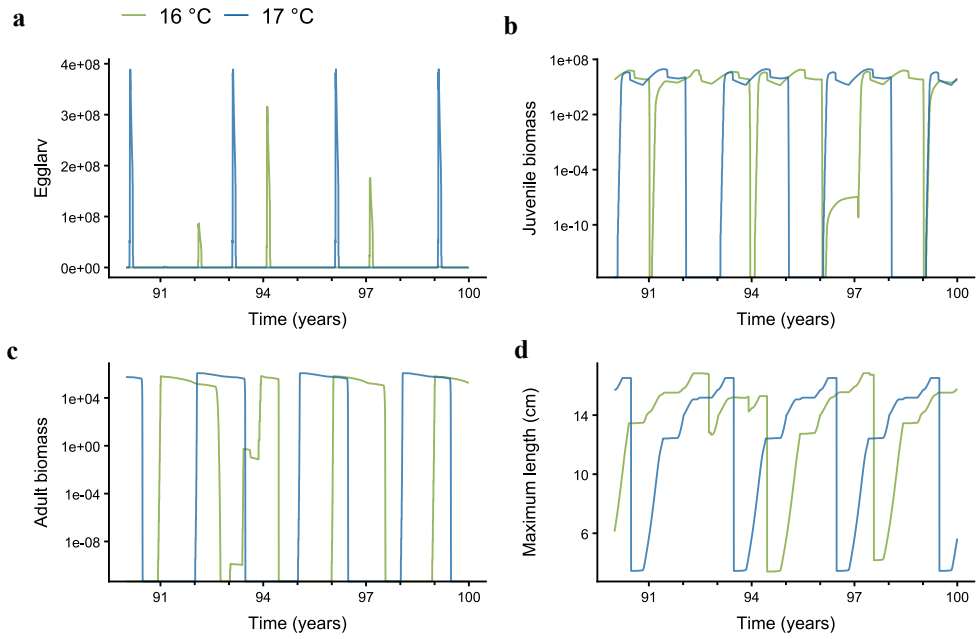


Figure A19: Variation in Egglarv (total amount of released eggs and larvae) (non-log) (a), juvenile biomass (log) (b), adult biomass (log) (c), and maximum length (non-log) (d) of herring across time (years), at 16 °C and 17 °C.

Egg survival herring

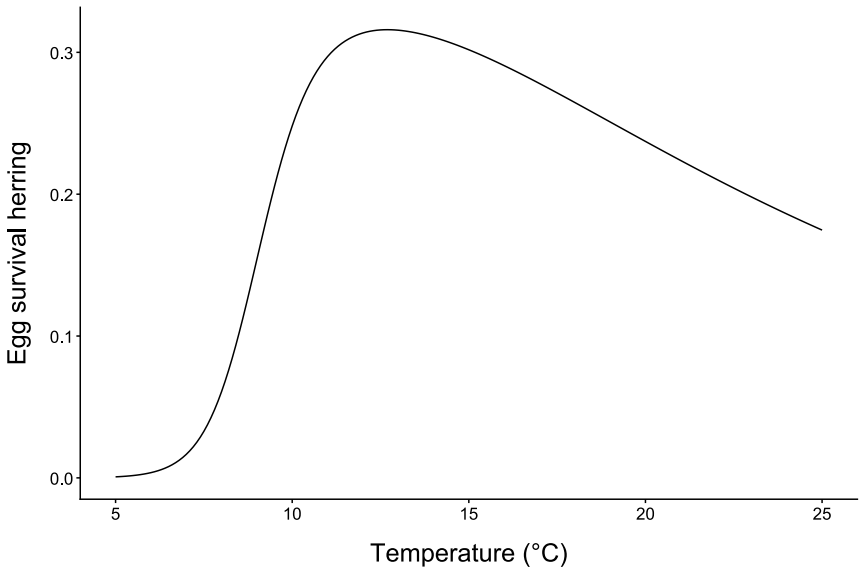


Figure A20: Egg survival of herring as a function of temperature (°C).

Herring biomass at 20 °C and 21 °C

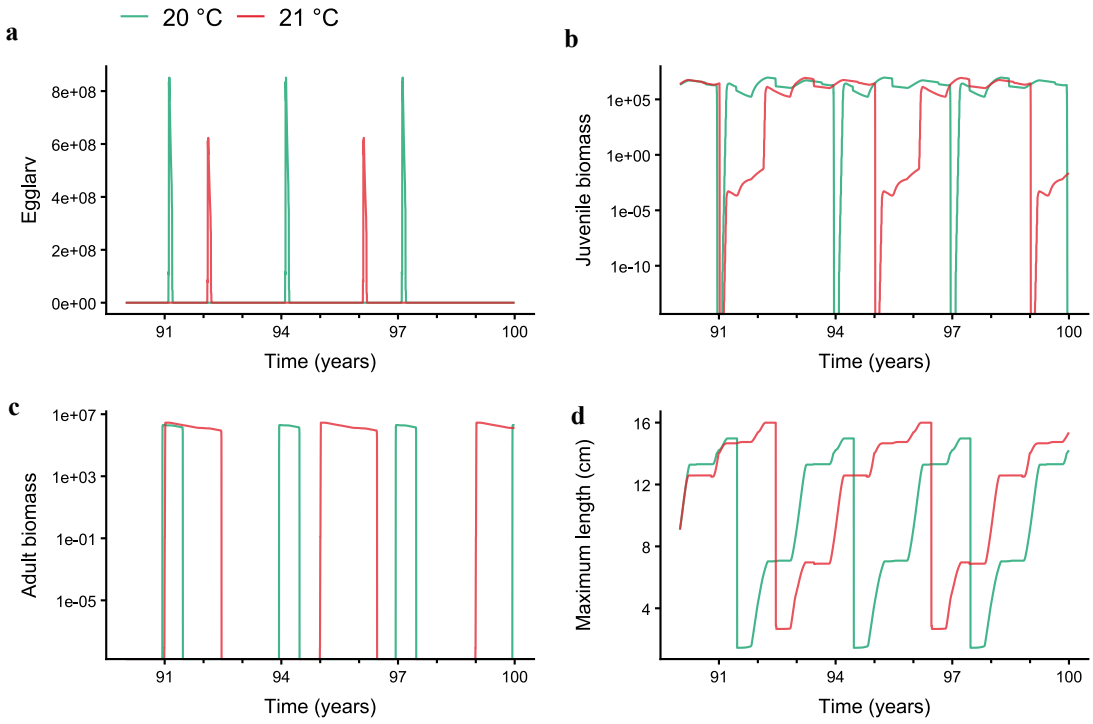


Figure A21: Variation in Egglarv (total amount of released eggs and larvae) (non-log) (a), juvenile biomass (log) (b), adult biomass (log) (c), and maximum length (non-log) (d) of herring across time (years), at 20 °C and 21 °C.

Handling time for herring

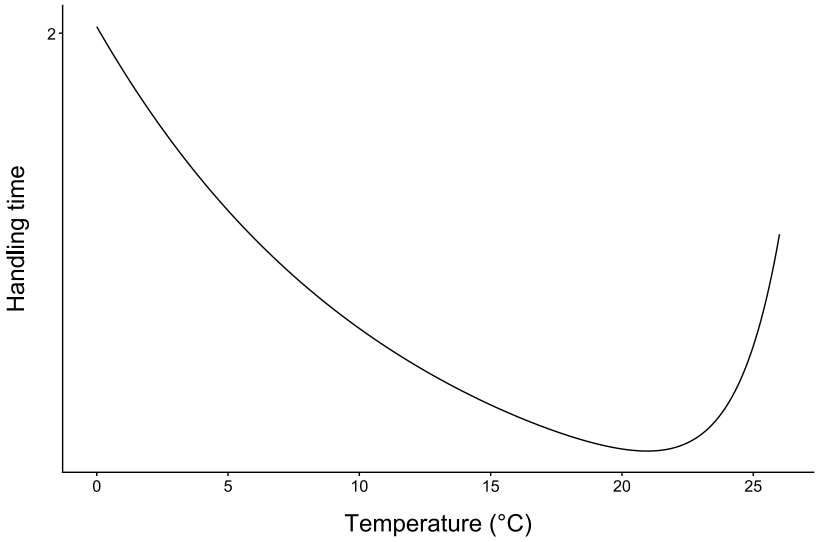


Figure A22: Handling time for herring as a function of temperature (°C).

Comparing herring dynamics with and without cod at 8 °C

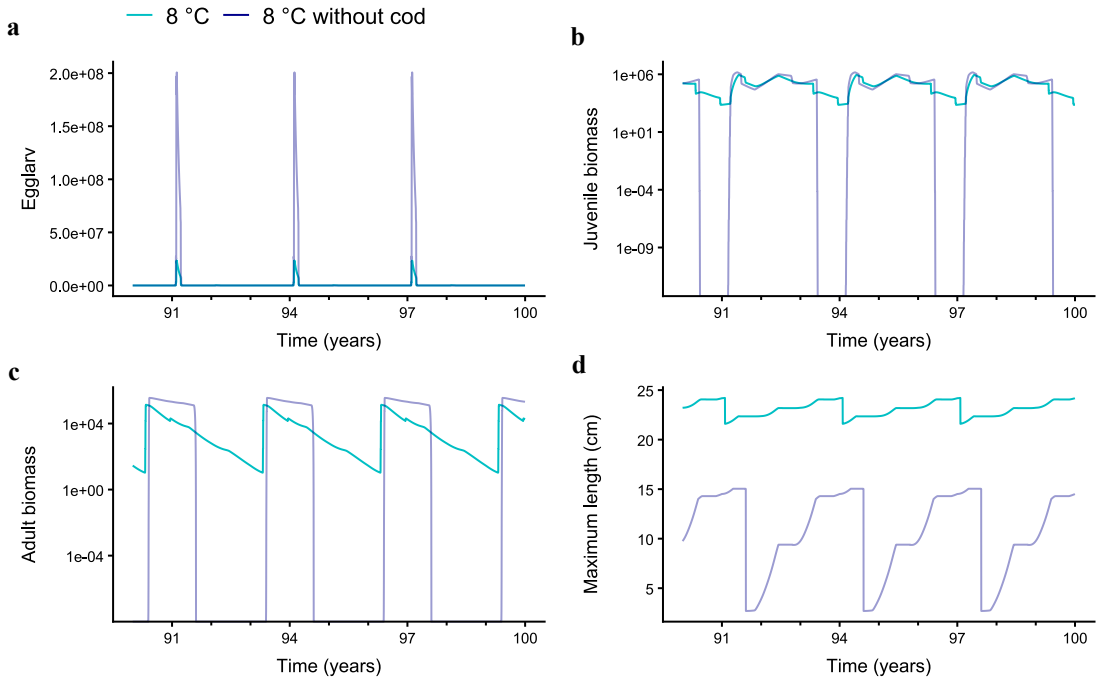


Figure A23: Comparing herring dynamics with and without cod in the model at 8 °C. Variation in Egglarv (total amount of released eggs and larvae) (non-log) (a), juvenile biomass (log) (b), adult biomass (log) (c), and maximum length (non-log) (d) of herring across time (years).

Comparing herring dynamics with and without cod at 15 °C

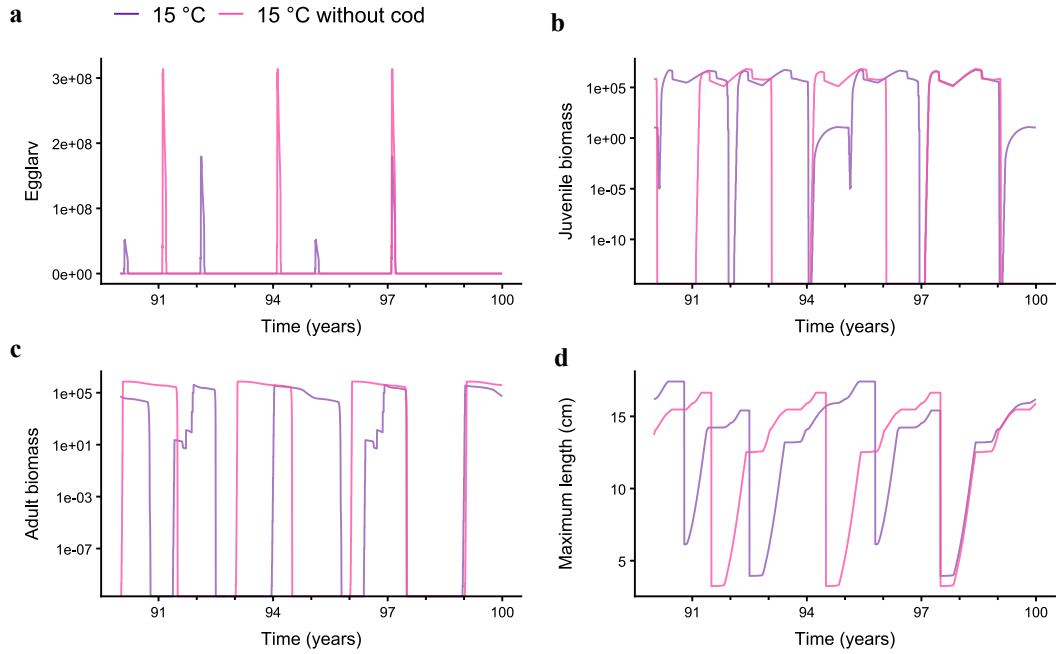


Figure A24: Comparing herring dynamics with and without cod in the model at 15 °C. Variation in Egglarv (total amount of released eggs and larvae) (non-log) (a), juvenile biomass (log) (b), adult biomass (log) (c), and maximum length (non-log) (d) of herring across time (years).

Comparing cod dynamics with and without herring at 8 °C

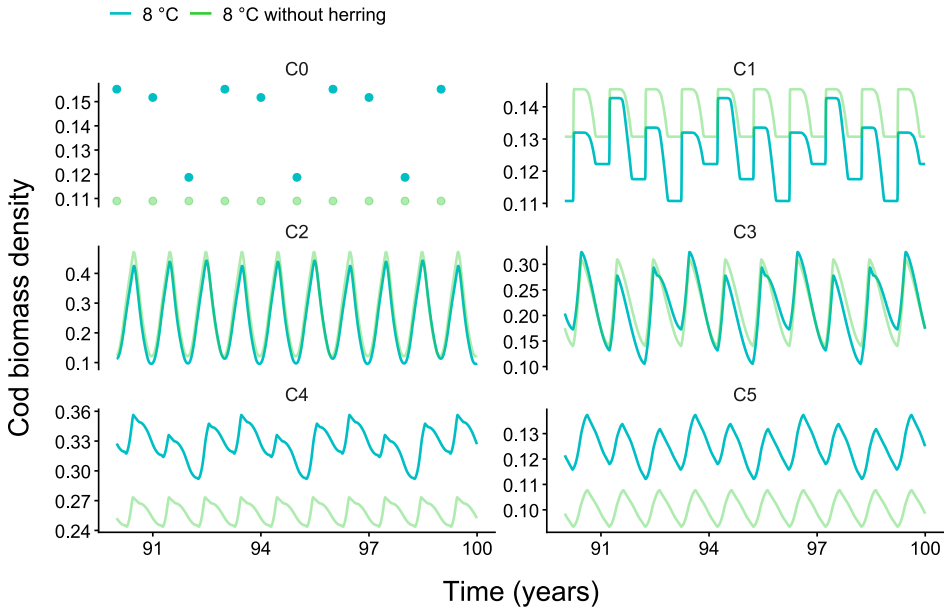


Figure A25: Cod with and without herring in the model at 8 °C. Cod biomass density (non-log) across time (year) for each cod stage (C1, C2, C3, C4, C5) and the number of eggs at the beginning of the reproduction period (C0).

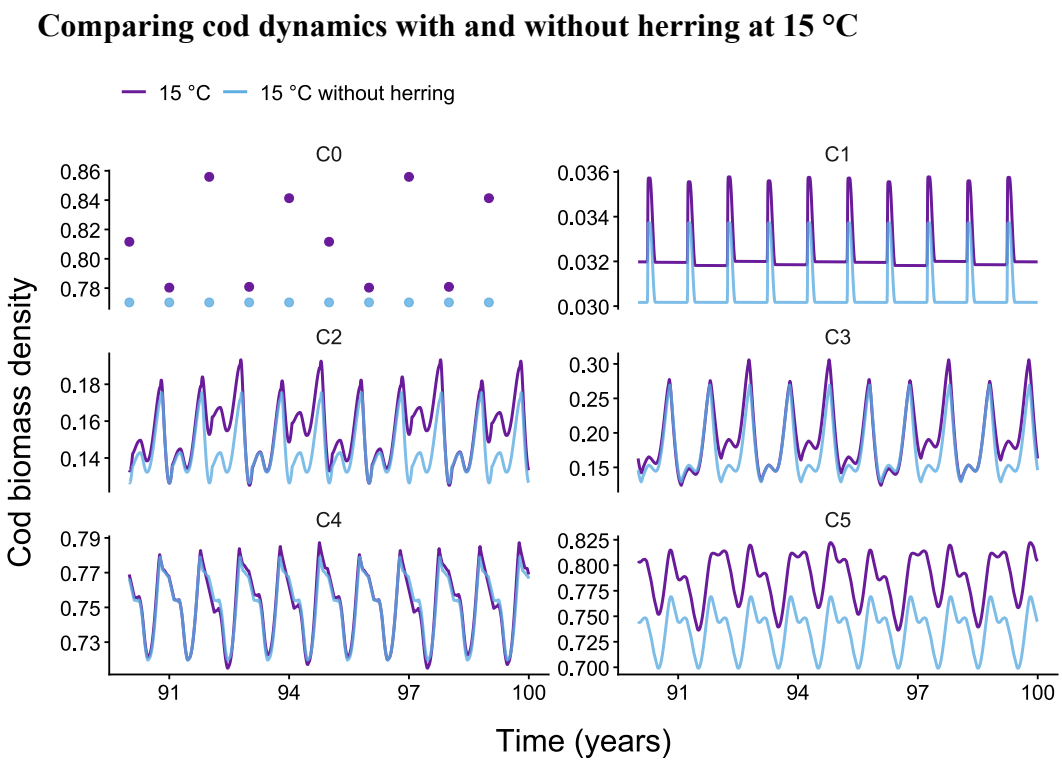


Figure A26: Cod with and without herring in the model at 15 °C. Cod biomass density (non-log) across time (year) for each cod stage (C1, C2, C3, C4, C5) and the number of eggs at the beginning of the reproduction period (C0).

Publishing and archiving

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