PRIMARY RESEARCH ARTICLE

Nonlinearity in interspecific interactions in response to climate change: Cod and haddock as an example

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Abstract

Climate change has profound ecological effects, yet our understanding of how trophic interactions among species are affected by climate change is still patchy. The sympatric Atlantic haddock and cod are co-occurring across the North Atlantic. They compete for food at younger stages and thereafter the former is preyed by the latter. Climate change might affect the interaction and coexistence of these two species. Particularly, the increase in sea temperature (ST) has been shown to affect distribution, population growth and trophic interactions in marine systems. We used 33-year long time series of haddock and cod abundances estimates from two data sources (acoustic and trawl survey) to analyse the dynamic effect of climate on the coexistence of these two sympatric species in the Arcto-Boreal Barents Sea. Using a Bayesian state-space threshold model, we demonstrated that long-term climate variation, as expressed by changes of ST, affected species demography through different influences on density-independent processes. The interaction between cod and haddock has shifted in the last two decades due to an increase in ST, altering the equilibrium abundances and the dynamics of the system. During warm years (ST over ca. 4°C), the increase in the cod abundance negatively affected haddock abundance while it did not during cold years. This change in interactions therefore changed the equilibrium population size with a higher population size during warm years. Our analyses show that long-term climate change in the Arcto-Boreal system can generate differences in the equilibrium conditions of species assemblages.

KEYWORDS
Bayesian statistic, climate variation, Gompertz model, intraspecific and interspecific competition, threshold modelling

1 | INTRODUCTION

The interactions among species can shift repeatedly as a result of changes in the environment. While environment conditions are continually fluctuating (e.g. temperatures alternate from low to high at a seasonal basis), climate warming is creating a directional change (e.g. towards high temperatures). Since the early 1990s, global temperatures have been steadily increasing, and these changes have been a major motivation for investigating a pletora of effects on biological systems, for example, distribution, behaviour, phenology and interaction

of plants and animals (Durant, Krasnov, Nikolaeva, & Stenseth, 2012; Ives, 1995; Parmesan & Yohe, 2003; Rosenzweig et al., 2008). Recently, it was suggested that indirect effects of climate change, that is, altered species interactions, may be more important for population dynamics than the direct effects (Ockendon et al., 2014; Stige, Ono, Eriksen, & Dalpadado, 2019). For example, changes in temperature may alter the behaviour and productivity of organisms which, in turn, may alter species interactions (Doney et al., 2012). Climate warming is thought to affect local populations in marine systems by altering the interaction between a species and its competitors, mutualists, predators, prey or even pathogens (Lubchenco et al., 1991). However, the strength of the interaction may vary through time particularly in changing environment (Stenseth et al., 2002) due to, for example, changes in the resource availability (Lima, Previtali, & Meserve, 2006) and presence or absence of the interacting species.

High latitude regions are highly sensitive to climate change and the Boreal-Arctic seas are already changing drastically (Johannesen et al., 2012). According to the Intergovernmental Panel on Climate Change, the temperature in the Arctic increases faster than other areas and will likely continue to increase further in the future leading to a borealization of the system (Fossheim et al., 2015; Frainer et al., 2017). More specifically, in the Barents Sea, a marginal sea of the Arctic Ocean, summer temperature will possibly increase between 2°C and 4°C by the mid-21 century (Sandø, Johansen, Aglen, Stiansen, & Renner, 2020). High latitude regions are thus ideal systems to study the effect of climate change (e.g. warming) on species interaction. Atlantic haddock (*Melanogrammus aeglefinus*) and cod (*Gadus morhua*) are two gadoid species of high economic importance, closely related, that co-occur in many regions in the North Atlantic such as the Barents Sea (Jakobsen & Ozhigin, 2011), the North Sea (Hedger et al., 2004; Høines & Bergstad, 1999) and the Georges bank (Buckley, Calidarone, & Lough, 2004). Haddock and cod are potential competitors at the larval stage having an overlapping diet (Høines & Bergstad, 1999; Kane, 1984) but are more segregated when adults (Jakobsen & Ozhigin, 2011). Cod is, however, known to prey on haddock in the Barents Sea (Durant et al., 2014; Jakobsen

& Ozhigin, 2011) where the weight portion of haddock in cod diet is about 6%–14% (Holt, Bogstad, Durant, Dolgov, & Ottersen, 2019; ICES, 2018).

Here, we explore the effect of year-to-year variation in climatic condition on the interaction between species using the Northeast Arctic (NEA) haddock and NEA cod stocks in the Barents Sea as an example. Both stocks are currently growing (ICES, 2018), expanding their distribution area northward (see Figure S1), and have a partially overlapping diet (Jakobsen & Ozhigin, 2011) which may affect the strength of their interaction and the resulting population dynamics. NEA haddock mature in the Barents Sea at age 4–7 years (Bergstad, Jørgensen, & Dragesund, 1987). The mature haddock migrate to spawn in March to June along coastal banks and on the slope between the continental shelf off north-western Norway and the deep Norwegian Sea from 62 to 70°N (Jakobsen & Ozhigin, 2011). The NEA cod mature at age 7–11 (Ottersen, Hjermann, & Stenseth, 2006) and migrate to the coast of Norway to spawn in February to early May (Langangen et al., 2019). Climate indices and regional scale hydroclimatic variables have previously been used as environmental drivers to explain gadoid population growth (Durant et al., 2013) and particularly in the Barents Sea for cod and haddock (Durant & Hjermann, 2017). Climate indices, such as the North Atlantic Oscillation index for the winter months (NAO; Hurrell & Deser, 2009), capture complex spatio-temporal variability into a simple metric and integrate larger-scale climate processes and their variability (Hallett et al., 2004). They have been shown to be good predictors for biological processes (Stenseth, Ottersen, & Hurrell, 2003). In the Barents Sea, NAO was documented affecting different component of the system such as NEA cod (Hjermann et al., 2007).

Temperature is a regional hydro-climatic variable potentially affecting the survival and growth of early life stages (Dingsør, Ciannelli, Chan, Ottersen, & Stenseth, 2007; Langangen et al., 2014) as well as their distribution (Hidalgo et al., 2012) and recruitment (Ottersen et al., 2013). In the Barents Sea, the Kola transect temperature is representative of the Atlantic water masses in the south-central Barents Sea (Ingvaldsen, Loeng,

TABLE 1 Summary of the equations

	Equation formulation		Eqn.
Theory	$\ln(N_{i,t+1}) =$	$a_{i0} + (1 + a_{ii})\ln(N_{i,t}) + a_{ij}\ln(N_{j,t})$	T1
	$\ln(N_{i,t+1}) =$	$\begin{cases} a_{i0} + (1 + a_{ii})\ln(N_{i,t}) + a_{ij}\ln(N_{j,t}) \text{ if } \theta_t < \theta \\ b_{i0} + (1 + a_{ii})\ln(N_{i,t}) + b_{ij}\ln(N_{j,t}) \text{ otherwise} \end{cases}$	T2
Model	$\ln(Cod_{t+1}) =$	$a_{c0}(ST_t, NAO_t) + (1 + a_{cc})\ln(Cod_t) + a_{ch}\ln(Had_t)$	M1
	$\ln(Had_{t+1}) =$	$\begin{cases} a_{h0}(ST_t, NAO_t) + (1 + a_{hh})\ln(Had_t) + a_{hc}\ln(Cod_t) \text{ if } ST_t < \theta \\ b_{h0}(ST_t, NAO_t) + (1 + a_{hh})\ln(Had_t) + b_{hc}\ln(Cod_t) \text{ otherwise} \end{cases}$	M2

Note: The two first equations correspond to the theoretical reparametrized and log-transformed Gompertz model (see Supporting Information model description) for equation T1 and the corresponding thresholded formulation (equation T2). The environmental variable θ_t is used as a threshold to partition the effect of 'low' or 'high' environmental regime (e.g. if θ interacts with N_j, (a_{ij}) will differ from (b_{ij}), as can a_{i0} from b_{i0} while a_{ii} will remain unchanged). The remaining two equations (equations M1 and M2) correspond to the models used for cod and haddock in the study, respectively, where $a_{c0}(ST_t, NAO_t) = a'_{c0} + a_{c,ST} ST_t + a_{c,NAO} NAO_t$ and $a_{h0}(ST_t, NAO_t) = a'_{h0} + a_{h,ST} ST_t + a_{h,NAO} NAO_t$ while $b_{h0}(ST_t, NAO_t) = b'_{h0} + b_{h,ST} ST_t + b_{h,NAO}$ NAO_t with in our case $a_{h,ST} = b_{h,ST}$ and $a_{h,NAO} = b_{h,NAO}$. Cod_t and Had_t are the abundance for cod and haddock at time t, respectively, and θ is the threshold for ST = 4.05°C. Subscript 'h' is for haddock, 'c' for cod and 't' for time/year.

Ådlandsvik, & Ottersen, 2003) and explain the dynamics for NEA cod (Hjermann, Stenseth, & Ottersen, 2004) and northward population displacement in the Barents sea of both cod and haddock (Fall, Ciannelli, Skaret, & Johannesen, 2018; Landa, Ottersen, Sundby, Dingsør, & Stiansen, 2014). Both NAO and sea temperature (ST) are classically used in population dynamics studies for the cod and haddock and well documented as affecting the change of population in the studied system (Frainer et al., 2017; Johannesen et al., 2012), particularly at early life stages (Stige et al., 2010), and other fish (Ottersen, Kim, Huse, Polovina, & Stenseth, 2010).

We use a discrete-time Gompertz density-dependent model (Table 1), a model that is widely used across marine (Langangen et al., 2017; Myers & Cadigan, 1993; Myers, Mertz, & Barrowman, 1995) and terrestrial (Bjørnstad, Fromentin, Stenseth, & Gjøsæter, 1999; Durant et al., 2012; Stenseth et al., 1999, 2015) systems, where intraspecific and interspecific interactions affect each species' population density. In particular, we use a Gompertz state-space model (Ono, Langangen, & Stenseth, 2019) and used two sources of population estimates: scientific bottom trawl surveys and acoustic surveys.

Our aims are (a) to assess whether the interaction between cod and haddock is changing over time, (b) to establish, if this change is linked to any changes in climatic variables and (c) to understand what it means for the population dynamics in the system.

2 | MATERIALS AND METHODS

2.1 | Data

The study was conducted on NEA haddock and NEA cod populations from the Barents Sea; the data (1981–2018) were extracted from fish stock assessments reported by the International Council for Exploration of the Seas (ICES; tables B1 and B3 for the haddock, tables A3 and A13 for the cod; ICES, 2018). The data are stock abundances estimated from the Joint winter Barents Sea acoustic survey in January–March and abundance indices from the winter bottom trawl surveys (1981–2018) in the Barents Sea for haddock. For cod, the data reported by ICES are the sum of acoustic abundance estimates from the Joint winter Barents Sea survey and the Norwegian Lofoten acoustic survey (1985–2018), and the abundance index from the Norwegian bottom trawl survey (1981–2018) in the Barents Sea in January–March (Figure 1). For both species, ICES reported yearly total abundance that corresponds to the sum of abundances for fish of age 1 and older (ICES, 2018).

Two climatic variables (the ST and the NAO) were used as potential environmental drivers of haddock and cod population dynamics (e.g. Durant et al., 2013; Durant & Hjermann, 2017; Hjermann et al., 2007; Landa et al., 2014; Ottersen et al., 2013; Figure 1). The ST (1921–2017) is an aggregated average of several depths (1–200 m) at five stations on the Kola meridian transect (33°30′E, 70°30′–72°30′N) in the Barents Sea (http://www.pinro.ru/). The

NAO, calculated for the winter months (Hurrell & Deser, 2009), represents North Atlantic-scale climate effects (1964–2018).

We used the data from 1985 only (period 1985 to 2017; i.e. 33 years) ensuring that we had each year both trawl and acoustic data for both species to model.

2.2 | Model description

We needed a model formulation that should be able to capture both the complexities of species interactions and density-dependent regulation and easily interpreted by a general readership. All subsequent analyses were based on Gompertz models that incorporated the effect of interspecific and intraspecific competition as well as environmental variables. The textbook example of the Gompertz model (Gompertz, 1825) is written as follows:

$$N_{i,t+1} = N_{i,t} \exp\left[r_i\left(1 - \left[\alpha_{ii}\ln\left(N_{i,t}\right) + \alpha_{ij}\ln\left(N_{j,t}\right)\right]/K_i\right)\right], \qquad (1)$$

where r_i is the maximum per-capita (intrinsic) growth rate for species i, K_i is the local equilibrium density in the absence of heterospecifics and α_{ij} represents the per-capita effect of species j on the growth rate of species i. Typically, K, r and α are considered constants for a given species, location and environmental condition, respectively.

Model (1) can be re-parameterized as follows:

$$N_{i,t+1} = N_{i,t} \exp\left[a_{i0} + a_{ii}\ln\left(N_{i,t}\right) + a_{ij}\ln\left(N_{j,t}\right)\right], \qquad (2)$$

where $a_{i0} = r_i$, $a_{ii} = -r_i/K_i$, and $a_{ij} = -r_i\alpha_{ij}/K_i$, and where $\alpha_{ii} = 1$. That is, the ecological parameters can be expressed as statistical parameters: $r_i = a_{i0}$, $K_i = -a_{i0}/a_{ii}$, and $\alpha_{ij} = a_{ij}/a_{ii}$.

Model (2) on the log-scale, and slightly rearranged becomes:

$$\ln\left(N_{i,t+1}\right) = a_{i0} + \left(1 + a_{ii}\right)\ln\left(N_{i,t}\right) + a_{ij}\ln\left(N_{j,t}\right), \qquad (3)$$

which is equation T1 (Table 1). This model expresses changes in log-population size for species i, $\ln(N_{i,t})$, over annual time step t, as a function of its growth potential a_{i0}, a density-dependent effect on population increase a_{ii}, and a competition/predation effect of species j on species i, a_{ij}.

2.3 | The Gompertz state-space model

For the Gompertz state-space model, a Gaussian distributed stochastic term with variance σ^2_{proc} was added to the model to acknowledge the lack of data availability and our imperfect understanding of the complex dynamics of the populations.

$$\ln\left(N_{i,t}\right) \sim \text{Normal}\left(a_{i0} + \left(1 + a_{ii}\right)\cdot\ln\left(N_{i,t-1}\right) + a_{ij}\cdot\ln\left(N_{j,t-1}\right), \sigma^2_{proc}\right). \quad (4)$$

However, we can seldom observe the true population, but rather have an index of population abundance. We assumed that the abundance
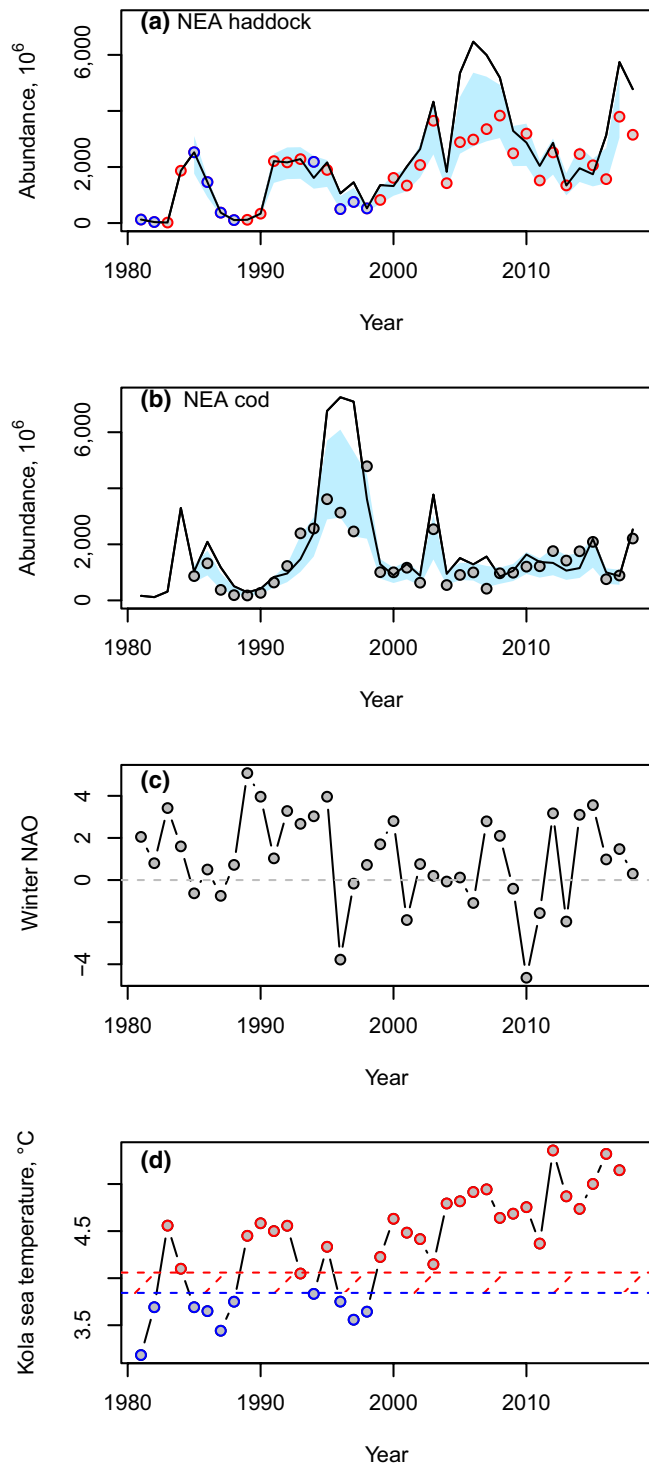
FIGURE 1 Time series of population abundance of NEA haddock (a) and NEA Arctic cod (b), North Atlantic Oscillation (NAO) calculated for the winter months (c) and average sea temperature (ST) aggregated over several depths (1–200 m) (d). For plots (a) and (b), lines are abundance indices from bottom trawl surveys and dots are indices from acoustic survey. For NEA haddock, acoustic data are circled in blue for the years with temperature under the estimated threshold between >3.83°C and ≤4.05°C. The blue bands are the 95% credibility intervals of our model for the years 1985–2017. Note that the abundance estimates (with the credibility intervals) cannot be directly be compared to the abundance indices as they do not take into account the observation errors nor the scaling coefficient (β, methods and Table 3; Figure S3). For plot (d), the threshold ST between >3.83°C and ≤4.05°C is shown with a dashed area. The red dots are the yearly value of ST over the threshold and the blue dots the yearly values under it

2.4 | Thresholded Gompertz state-space model

To detect possible nonlinear effect of climatic variable to the population dynamics, we tested for potential interactions between the explanatory variables using the Bürmann's expansion (Chan, Kristoffersen, & Stenseth, 2003) for the trawl data and acoustic data separately (Stenseth et al., 2015). When nonlinearity was detected, we included a threshold non-additive effect in the Gompertz state-space model (Table 1, equation T2) where the species growth potential and the competition/predation effect (b_{j0} and b_{ji}, respectively) changed according to whether the climate covariate (ST) was above or below some threshold level θ (see Supporting Information for implementation detail).

To detect possible threshold value, the model did as follows: (a) looped over each climate covariate value in the data and set it as the new threshold in the model and (b) estimated model parameters and calculated the corresponding process model log-likelihood. If any covariate values stood out as potential threshold values, the corresponding log-likelihood would be larger. In this search process, we only used climate covariate values within the 20 and 80 percentiles (19 values used out a total of 33) to remove any 'border' effect, that is, spurious result due to very unequal partition of climate condition (e.g. 95% below threshold vs. 5% above). The modelling approach only selects the threshold value from the available data, that is, T. The real threshold value is therefore $\leq\theta$ and $>\theta_b$; with θ_b being the first value lower than the selected θ.

2.5 | Parameters estimation and dynamics interpretation

We used a Bayesian Markov chain Monte Carlo (MCMC) approach to jointly estimate all parameters (for both haddock and cod) in the model for the period 1985–2017. For this purpose, we used the software Stan through the R packages *rstan* and *shinystan* (The

indices (derived from the trawl and acoustic surveys) were normally distributed (in log scale) with variance term, σ^2_{trawl} (and $\sigma^2_{acoustic}$) around the true log population values. We included a scaling coefficient β (on ln scale) for the trawl index to account for possible scaling issues between these two sources of data.

$$\ln\left(O^{acoustic}_{i,t}\right) \sim \text{Normal}\left(\ln\left(N_{i,t}\right), \sigma^2_{acoustic}\right), \quad (5)$$

$$\ln\left(O^{trawl}_{i,t}\right) \sim \text{Normal}\left(\beta \cdot \ln\left(N_{i,t}\right), \sigma^2_{trawl}\right). \quad (6)$$

Stan Development Team, 2014). A likelihood function was created based on the model and data (acoustic and trawl abundance estimates at the same time), and in combination with the prior distributions of the parameters, the posterior distributions were estimated. Weakly informative priors were used to let the data drive the inferences. We used three independent chains with 200,000 iterations each, where the first 120,000 iterations were used as 'burn-in' iterations to ensure that the chains had converged. In addition, we thinned the chains with a factor 10 to reduce autocorrelation in the posterior samples and to produce a reasonable amount of output. We used the Gelman and Rubin $\hat{R}$ convergence diagnostics (Gelman & Rubin, 1992), visual inspection of the chains, and posterior predictive checks to ensure convergence and model fit. The R codes developed for the study are found in the Supporting Information.

Using the entire MCMC samples, we calculated the ecological parameters and the associated uncertainty for species i from the estimated statistical parameters; $a_{i0} = r_i$ (maximum per-capita haddock growth rate), $-a_{i0}/a_{ii} = K_i$ (the local equilibrium density in the absence of heterospecific effect), and $a_{ij}/a_{ii} = \alpha_{ij}$ (interspecific per-capita effect). See Table 2 and Supporting Information for correspondence between the ecological parameters and statistical parameters. We used the mean values of α_{ij} and K_i to plot the zero-growth isoclines (Stenseth et al., 2015) and calculated the equilibrium abundances N^*. We calculated two Jacobian matrices (under and over the threshold) and the corresponding dominant eigenvalues λ for each sample (Fowler, 2010). Using the eigenvalues, we classified the dynamical properties of the system above and below the threshold.

All analyses were conducted using the software R v.3.5.2 (R Core Team, 2018).

3 | RESULTS

For haddock, the Bürmann test indicated an interaction between the effect of cod abundance on haddock and ST for both trawl and acoustic data ($p < .05$). We thus modelled haddock with a non-additive model (Table 1, equation T2) with an interaction between the effect of cod abundance on haddock and ST (Table 1, equation M2). The model estimated a temperature threshold θ between >3.83°C and ≤4.05°C (Figure S2). For cod, the Bürmann test found no interaction with any environmental variable and we used the additive model (Table 1, equations T1 and M1).

Visual inspection of the chains suggested that the model had converged; the three parallel Hamiltonian Monte Carlo chains were well mixed, had low autocorrelation after thinning and showed no trends after the burn-in iterations. There were no warnings of divergent transitions in the chains. The Gelman and Rubin $\hat{R}$ convergence diagnostics were between >0.999 and <1.002 for all model parameters, providing additional support for convergence. Additionally, the model captured the variability in the four observed time series well, with no systematic deviations between fitted and observed values (Figure S3).

Average parameter estimates from these models are given in Table 2 (Figure S4). Using these parameters, we calculated K and α which were used to plot the zero-growth isoclines (Figure 2).

For haddock, climate change, as expressed by ST, had a biologically important effect (Table 1, equation M2). The interspecific competition term—the effect of cod numbers on haddock per-capita growth rate—was significantly negative (b_{hc}) when ST was over the temperature threshold θ and significantly positive (a_{hc}) under the threshold (Table 2). In years when ST were colder than the estimated threshold temperature, median $\alpha_{hc} = -1.11$; while in years in which temperatures were

TABLE 2 Average estimated parameter values for the haddock and cod models

Species	Term	Mean estimate	5%	95%	Sig
NEA haddock	$a'_{h0} = r_h \, (ST_t < \theta)$	−0.631	−3.250	2.384	
	$b'_{h0} = r_h \, (ST_t \geq \theta)$	5.960	3.636	8.241	*
	$1 + a_{hh} = 1 - r_h/K_h$	0.617	0.389	0.844	*
	$a_{hc} = -r_h\alpha_{hc}/K_h(ST_t < \theta)$	0.419	0.035	0.775	*
	$b_{hc} = -r_h\alpha_{hc}/K_h(ST_t \geq \theta)$	−0.445	−0.830	−0.052	*
	$a_{h,ST}$	0.219	−0.100	0.600	
	$a_{h,NAO}$	−0.025	−0.095	0.045	
NEA cod	$a'_{c0} = r_c$	1.115	−0.728	3.025	
	$1 + a_{cc} = 1 - r_c/K_c$	0.593	0.276	0.892	*
	$a_{ch} = -r_c\alpha_{ch}/K_c$	0.233	−0.018	0.491	·
	$a_{c,ST}$	−0.082	−0.329	0.160	
	$a_{c,NAO}$	0.047	−0.031	0.124	

Note: In 'term' is also indicated the equivalence between the statistical parameters estimated and ecological parameters of the Gompertz model: r (maximum per-capita (intrinsic) growth rate), K (local equilibrium density in the absence of heterospecifics) and α (per-capita effect interaction) as described in the Supporting Information model description. Subscript 'h' stands for haddock and 'c' stands for cod. * indicates the parameters that are significant (i.e. the credibility interval does not include 0, see Figure S4). · indicates a $p < .10$.
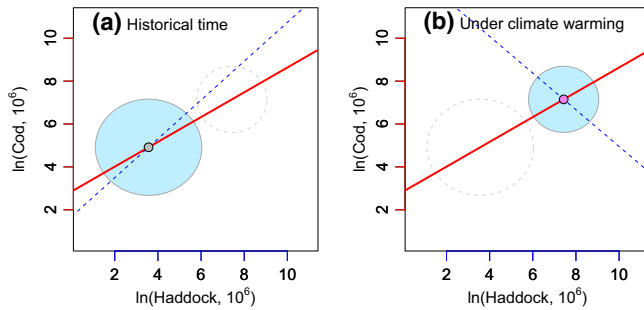
FIGURE 2 Zero-growth isoclines for sympatric populations of Northeast Arctic (NEA) haddock (blue dashed lines) and NEA cod (bold red line). The haddock stock shows a threshold interaction with an environmental variable (ST) and has two isoclines (and equilibrium states) for ST below (a) and above (b) threshold between >3.83°C and ≤4.05°C, grossly corresponding to the historical situation and the present situation, that is, under climate warming. The dot shows the estimated stable equilibrium point N^* and the ellipses illustrate the 95% deviation around the equilibriums calculated using all Markov chain Monte Carlo posterior values. For the purpose of comparison, the ellipse of plot (b) is presented in grey shade in plot (a) and reciprocally

warmer $\alpha_{hc} = 1.17$ (Table S1). In addition, the maximum per-capita haddock growth rate (r_h) increased on average from −0.631 to 5.960, when ST was over the threshold resulting in an increased intraspecific competition. Therefore, ST changes are affecting both intraspecific and interspecific competition for haddock. The environmental variables (ST and NAO) did significantly affect the haddock abundance only through the temperature threshold effect (Table 2).

For cod, the statistical parameter for the interspecific term a_{ch}, expressing the effect of haddock numbers on cod per-capita growth rate, was significantly positive indicating a covariation (Table 2). The corresponding ecological parameters median was $\alpha_{ch} = -0.57$ (Table S1). The environmental variables did not significantly affect the cod abundance in the studied years (Table 2).

Using the entire set of individual MCMC samples (24,000), the population stability for haddock and cod was then examined (equilibrium abundances [N_i^*] and eigenvalues [λ_i]) (Stenseth et al., 2015) and associated uncertainty calculated (Table S1). The equilibrium abundance N_i^* being all positives indicated that the system was feasible. For ST $< \theta$, the two average eigenvalues of the Jacobian matrix were $\lambda_{Had} = -0.08$ and $\lambda_{Cod} = -0.71$ indicating a stable node equilibrium (Edelstein-Keshet, 2005). For ST $\geq \theta$, $\lambda_{Had} = \lambda_{Cod} = -0.40 \pm i0.32$ indicating a stable focus equilibrium which means that the pathway of approach to the equilibrium is oscillatory with a decreasing amplitude (Table S1).

4 | DISCUSSION

Using long-term population time series coupled with environmental covariates in a state-space framework, we have demonstrated that climate change, that is, ocean warming, can alter the interaction between cod and haddock thus altering the equilibrium densities

between the two species. The consequences of climate change on the strength of interaction between species are less studied than, for example, its direct effect on population dynamics (Bertness & Ewanchuk, 2002; Durant & Hjermann, 2017; Durant et al., 2019; Stenseth et al., 2004; Stige et al., 2014). Here we illustrated how species interactions might be drastically modified with climate change. Notably, we found empirical evidence for nonlinear change in species interaction (Table 1) directly linked to climate warming; that is, increase in the ST. This is consistent with studies suggesting that many marine ecosystems are increasingly susceptible to sudden nonlinear transformations due to climate warming (Hoegh-Guldberg & Bruno, 2010). Non-additive effect (e.g. threshold) of the environment (e.g. climate) on population dynamics has been observed in both terrestrial (Stenseth et al., 2004, 2015) and marine systems (Ciannelli et al., 2013; Dingsør et al., 2007; Lindegren, Checkley, Koslow, Goericke, & Ohman, 2018; Llope et al., 2011; Vasilakopoulos & Marshall, 2015) and may lead to different population equilibrium and dynamics (Stenseth et al., 2015). In our study, the nonlinearity did not lead to the exclusion of the predated species (i.e. the haddock; Figure 2) even if the abundance of the predator (i.e. the cod) was increasing. However, the nonlinear effect of long-term changes in ST interacted with population processes to swap the relative abundances of haddock and cod (Figure 2): cod have higher equilibrium abundance in cooler years, while haddock have the higher equilibrium abundance of the two stocks in warmer years. Notably, while both estimated equilibriums are stable (Figure 2; Table S1), when temperature is over the threshold the system can show a damped oscillations in abundance for both species that add to the variability. In addition, with increase in temperature both species are predicted to reach a higher equilibrium abundance than under the threshold which makes trophic cascades (down the food chain starting from the cod through the haddock) and restructuring of the local food web less probable (as for cod in Canada; Frank, Petrie, Choi, & Leggett, 2005). However, any climate-induced shifts in competition and predation can be expected to filter through the whole ecosystem, driving direct and indirect changes across multiple trophic levels (Fowler, 2010, 2013). The threshold effect lead to a change in the local equilibrium point when ST is above the threshold in any year. While a temperature drop below the threshold in subsequent years should lead to a change in the equilibrium and dynamical behaviour of the system, this is improbable under the current global warming (Figure 1d).

The NEA cod is a predator of haddock as shown by cod diet studies (Durant et al., 2014; Holt et al., 2019) and is expected to negatively affect the haddock stock. This is what we found for high ST. However, more importantly, our results indicated that cod effect on haddock that was positive becomes negative with the increase in ST, a trend of recent years (e.g. Gillett & Fyfe, 2013), suggesting a possible change in these species interaction. Indeed, recent analyses of Barents Sea cod stomach contents showed a significant increase in the proportion of haddock in their diet since 1984 (see Figure S5a; Holt et al., 2019). This change in diet may be linked to the distribution change of the two species with climate warming (Fossheim et al., 2015). This is particularly the case for younger age-class of

TABLE 3 Average estimated parameter values for the models

Model	Parameter	Mean	5%	95%
Haddock	Process error	0.449	0.312	0.609
	Observation error (acoustic)	0.187	0.041	0.309
	Observation error (trawl)	0.238	0.102	0.346
	β = Scaling coefficient (trawl)	1.027	1.014	1.039
Cod	Process error	0.527	0.388	0.694
	Observation error (acoustic)	0.360	0.183	0.511
	Observation error (trawl)	0.277	0.064	0.463
	β = Scaling coefficient (trawl)	1.037	1.017	1.057

haddock (<50 cm; Landa et al., 2014) that are the most frequent haddock in cod's stomach (Holt et al., 2019). This can also be related to the increase in the mean size of the NEA cod in recent years, the haddock being more present in the diet of larger cod than in smaller cod one (Holt et al., 2019). However, while the predation pressure from cod on haddock increases with temperature so does the haddock population growth (r in Tables 2 and 3). This indicates that the negative effect of increased cod predation on haddock is somehow compensated, maybe by the positive effect of the temperature increase. Indeed, both stocks seem to covariate with climate as shown by the increase in recruitment with temperature increase (Bogstad, Dingsør, Ingvaldsen, & Gjøsæter, 2013) that may partially explain the observed positive effect of cod on haddock during cold years. The haddock equilibrium density is increasing from 23 million to 1725 million individuals, the posterior mean population estimates for high ST being distributed around the equilibrium point (Figure 2). This situation may occur when the environmental conditions (in our case higher ST) are such that the productivity is more strongly increased than the predation pressure (hence reducing the apparent predation). Indeed, we observed a higher representation of capelin (*Mallotus villosus*) in the cod diet during warmer years than during cool years (Figure S5b); capelin being a key species in the Barents Sea with a distribution affected by ST change (Hop & Gjøsæter, 2013). In other words, the years when cod has a negative effect on haddock population correspond to the years when capelin is also more abundant in cod diet. This was confirmed when we explicitly included the effect of capelin abundance (as a covariate) on cod and haddock abundance in the Gompertz state-space model (Table S2). Capelin in the model had negligible effect for both cod and haddock and did not qualitatively change the estimates of other parameters. This means that while capelin is affecting the cod population, we did not find evidence that it is a proximate variable explaining the change of cod interaction with the haddock.

Similar to capelin, zooplankton biomass in the southern Barents Sea, preyed by both juvenile cod and haddock, is positively covariating with ST (Stige et al., 2014). With higher ST, the food availability for younger age fish is improving with expected increase in their growth (Langangen, Ottersen, Ciannelli, Vikebø, & Stige, 2016) and/or survival (Opdal, Vikebø, & Fiksen, 2011). Noteworthy is that the strength of the effect of haddock on itself is greater than the cod effect even during low ST periods (Tables 2 and 3). Note that the abundance data reported by ICES are calculated on estimated abundances from age 1 and older (ICES, 2018) and that the total abundance variability is principally driven by the youngest age abundance (ca. 70%). This means that any change of species interaction that affects age 1 may have a strong effect on haddock dynamics. Notably, both stocks showed and increased age/size structure during the last two decades (Durant & Hjermann, 2017; Ottersen et al., 2006) and particularly for cod that had a stock juvenation due to high fishing pressure towards the end of the 1970s (Ottersen, 2008). Increasing the mean size of the stock has an effect on the size spectrum of the prey eaten by the cod. For instance, 20 cm long cod feed on haddock up to ca. 12 cm long, whereas old 120 cm long cod can feed on up to 60 cm long haddock (Holt et al., 2019). Note that the proportion of haddock in the cod diet is also increasing with the cod size (Holt et al., 2019). However, while the age structure (i.e. size) changed in our study, the mean age of the spawning stock did not show any significant difference between cold and warm years (Figure S6) and may not explain the observed change of species interaction. On the other hand, cod being a generalist predator (Durant et al., 2014; Holt et al., 2019), the change of its diet (Figure S5) indicates a change in the community (Ellingsen et al., 2020). The species composition and abundance of cod prey vary over time in relation to environmental conditions and prey population dynamics (Durant et al., 2014). Cod follows the capelin northward with increase in temperature (Fall et al., 2018). The same increase in temperature positively affects the haddock stock size and lead young haddock northward in the Barents Sea (Landa et al., 2014) sustaining the overlap between the two species. At the same time, other prey are less represented in the cod diet such as shrimps *Pandalus borealis* (Holt et al., 2019) that may be remaining in the southern Barents Sea or undergo a slower poleward shifts in response to warming than the large, generalist, motile species, that are cod and haddock (Frainer et al., 2017).

In this study, we used a threshold model on two data sources to detect nonlinear responses in species interactions with climate change. Since the overlap between cod and haddock is widespread across the North Atlantic Ocean, our results may have important implications for all the co-occurring cod and haddock populations. The novel approach we developed to address potential nonlinearity in species interactions may also be applicable to many other systems, beyond the studied species. Non-additive population dynamics, that is, change in spawning biomass, linked to temperature or fishing have been previously described for many species. Cod stocks have been particularly studied in this respect due to the availability of long-term time series (Fauchald, 2010; Frank, Petrie, Fisher, & Leggett, 2011; Scheffer, Carpenter, Foley, Folke, & Walker, 2001; Sguotti et al., 2019; Vasilakopoulos & Marshall, 2015) but these studies did not address the nonlinearity of interaction with another species. The fact that

climate condition also affects the species interaction in a nonlinear way has implication for management and in particular for the ecosystem approach to fishery management (FAO, 2008), that takes into account the knowledge and uncertainties about biotic (e.g. other species abundance), abiotic (e.g. temperature) components of ecosystems and their interactions. In the Barents Sea, stocks assessments currently use some environmental information (e.g. haddock abundance, capelin abundance, cod predation and temperature; Skern-Mauritzen et al., 2016). Given the implication this can have on stock management, our approach may be highly timely and necessary. In particular, we have illustrated how a predator–prey/competitors system may change due to climate warming.

AUTHOR CONTRIBUTION

J.M.D. conceived, designed and led the analysis with input from Ø.L., K.O. and N.C.S. All authors discussed the results and commented the manuscript in terms of analysis, interpretation and writing.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Report of the Arctic Fisheries Working Group (AFWG) 18–24 April 2018 of the International Council for the Exploration of the Sea (ICES) at https://www.ices.dk/community/groups/Pages/AFWG.aspx; wNAO at https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based and Figure 1; and Kola ST in Figure 1.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.