

Increased early offspring growth can offset the costs of long-distance spawning migration in fish

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Constructing the Integral Projection Model (IPM)

For the construction of the IPM we assume a pre-reproduction annual census before the annual migration to the spawning grounds, so that offspring are counted as (nearly) 1 year olds. Each time step, a female produces a number of offspring, then, if it survives, grows to a new length (Vindenes et al. 2014). The surviving offspring will enter the model as 1-year olds (age-1 offspring) at the time of the census following a certain offspring length distribution (Figure S1).

This IPM is restricted for numerical and biological reasons to range from the length $L=0.01$ cm as the lower limit to the upper limit $U=200$ cm. These limits are well below/above the observed length range of cod. Very few offspring at age 1 will be smaller than 5 cm, since the offspring length distribution $L_1(y, d)$ is a normal length distribution, with a mean μ_{L_1} of 12.8 cm and standard deviation σ_{L_1} of 2 cm in the baseline model (Table S1; main text Figure 2d). Offspring length is independent of maternal length x but depends on migration distance d . The model was parameterized using length at age data (1980-2015), data on fishing mortality by age classes (mean of 1980-2014), and probability of maturity (ogives of maturity) (1980-2014) collected from the ICES AFWG Reports (ICES 2002, 2015). Data-at-age were converted to data-at-length by using the mean length at age (ICES 2002, 2015).

Survival function $S(x)$

Mortality estimates were based on instantaneous mortality estimates of early life stages (egg to larval stage) (Langangen et al. 2014) and cod in their first years of life (age 0.5-age 2) (Bogstad et al. 2015). For older stages, from age 3 onwards, mortality was calculated based on estimates by Ohlberger et al. (2014), with a natural mortality of 0.2 from age 4 onwards. Fishing mortality was included from age 3 (ICES 2015). A logistic function was fitted to the data points using non-linear regression.

$$S(x) = \frac{1}{1 + e^{-a_s(x-b_s)}} \frac{1}{1 + e^{-(-c_s(x-d_s))}} \quad (1)$$

Here, a_s as the slope (on logit scale), b_s defines the inflection point associated with the fastest increase in survival, c_s is the rate of decline associated with fishing mortality and d_s is the inflection point associated with the fastest decrease of survival (Table S1; main text Figure 2a).

To obtain a bounded model, the survival was defined to be zero at very large size (200 cm) (corresponding to approximately 30 years old cod, the highest theoretical age of cod (Tretyak

2000, Yaragina et al. 2011); note that cod older than 15 years are rarely found (Yaragina et al. 2011)).

Next year's length distribution $G(y; x)$

The mean length $\mu_g(x)$ calculation for the next year's length distribution $G(y; x)$ of fish from their second year of life (i.e. from age 1-2) onwards was conducted on growth increment values for mature cod at age 7 (Folkvord et al. 2014). The next year's length y was calculated by adding together the current length x and the increment value, and a linear model was fitted through those data points (with current length x as predictor). This resulted in the mean

$\mu_g(x) = a_g + b_g x$ for the normal distributed next year's length distribution $G(y; x)$. The standard deviation σ_g was set to 2 cm, the approximate value reported by Folkvord et al. (2014). Growth at age data were converted into growth at length, by using the mean length at age data from the years used in Folkvord et al. (2014) and the preceding cohorts (ICES 2015).

Offspring function $O(x, d)$

$$O(x, d) = e(x, d)pm(x)s_{first}0.5 \quad (1)$$

Where the parameters are defined as follows:

- Egg numbers $e(x, d)$ for the "Lofoten" baseline model:

$e(x, d = 780 \text{ km}) = e^{-15.09+3.595\ln(x)}$ from Marshall et al. (2006), assuming a constant body condition of the female. See next section for how migration distance effects are included

- Probability of maturity $pm(x)$ with a_{mat} as the slope and b_{mat} as the inflection point associated with the fastest increase in maturity (Table S1); fish smaller than 28 cm had 0 % maturity (reported maturity ogives > 0 for fish > 28 cm; ICES 2015).

$$pm(x) = \frac{1}{1 + e^{a_{mat}(b_{mat}-x)}} \quad (2)$$

- The survival probability for the first year of life, $s_{first} = 7.2 \cdot 10^{-5} \text{ year}^{-1}$ for the offspring function $O(x, d)$ was calculated by adding together mortality rates and transforming them to survival from the egg stage to age 1 with regard to the respective stage duration (Langangen et al. 2014, Bogstad et al. 2015). For obtaining the baseline model defined as having $\lambda(d = 780 \text{ km}) = 1$, we adjusted early stage survival (from egg to age 1) by scaling it with approximately 0.6 (reducing the λ from around 1.06 to 1.00).

Egg number adaptation according to migration distance

We assumed the fish start the migration with full energy stores $E_{max}(x)$ (Table S2 equation (1), Table S3). The energy stored and the somatic weight $W_{soma}(x)$ (Table S2 equation (2), Table S3) determined the total body mass $W(x)$ (Table S2 equation (3), Table S3) and thus the standard metabolic rate $SMR(x)$ (Table S2 equation (4), Table S3; Jørgensen & Fiksen 2006). The standard metabolic rate, the migration speed, and the duration of the migration $T_M(d)$ (Table S2, equation (5), depending of direction of migration) in turn determined the energy needed for the migration $E_M(x, d)$ (Table S2 equation (6), Table S3;

Jørgensen & Fiksen 2006). Since we assumed that the southwards migration is counter current with a current speed of $U_C = 0.1 \text{ m}\cdot\text{s}^{-1}$ (ICES 1994; Table S3), which is e.g. well within the range reported for the Norwegian Coastal Current (Haugan et al. 1991) we calculated the migration energy $E_M(x, d)$ separately for south- and northwards migration (Table S2, equation (5)) and summed it up. We assumed a swimming speed of $U_S = 0.3 \text{ m}\cdot\text{s}^{-1}$ (Table S3, Jørgensen & Fiksen 2006), leading to southwards swimming speed of $0.2 \text{ m}\cdot\text{s}^{-1}$ and northwards of $0.4 \text{ m}\cdot\text{s}^{-1}$ (ICES 1994, Jørgensen & Fiksen 2006, Jørgensen et al. 2008).

Using the baseline function for the Lofoten egg numbers (Marshall et al. 2006), we calculated the theoretical numbers of eggs which should be available, without any migration (“pre-migration” egg numbers), i.e. for migration distance $d = 0 \text{ km}$. We used the conversion of energy to egg numbers $0.256 \text{ eggs}\cdot\text{J}^{-1}$ (Jørgensen & Fiksen 2006) to calculate the egg numbers lost because of energy spent on migration $E_M(x, d)$.

$$e_{loss}(x, d) = 0.256 \frac{eggs}{J} E_M(x, d) \quad (4)$$

We added $e_{loss}(x, d = 780 \text{ km})$ to the egg numbers from the baseline model (see above; Marshall et al. 2006), which leads to the pre-migration egg numbers. Those are equal for all fish of a certain length. The egg numbers lost through the energetic costs caused by migrating a certain distance $e_{loss}(x, d)$ were subtracted from the pre-migration egg numbers. With this method we could calculate the egg numbers for both shorter or longer migration distance (d ranging from 300 km to 1600 km in our calculations, with 10 km steps) compared to the base line migration to Lofoten ($d = 780 \text{ km}$).

Size structure of the population

Using the IPM we analysed how the stable length distribution $w(x, d)$ of the population differed among three different spawning grounds in Finnmark ($d = 400 \text{ km}$), Lofoten ($d = 780 \text{ km}$) and Møre $d = 1500 \text{ km}$) after correcting for energetic costs of the migration and adjusting the offspring length to get equal fitness (measured by λ) across the different spawning grounds.

These results show that in our model predictions, Finnmark has the highest densities of small sized offspring with a distribution around the mean of the offspring length distribution of 12.2 cm (Figure S2). Equally, the offspring length distributions for Lofoten and Møre are shifted towards larger sizes, with larger, but fewer offspring due to increased mean offspring length, but also a decrease in offspring numbers due to the energy costs of longer migration (Figure S2). The cohorts of larger individuals are clearly visible for the Møre spawning ground, however the differences assimilate at larger sizes $> 100 \text{ cm}$ (Figure S2).

Robustness analyses

We tested the robustness of the model results using a one by-one perturbation of the parameters. All parameters of the survival function (Table S1) and the mean length μ_g (Table S1) of the length distribution $G(y; x)$ were changed by $\pm 10 \%$, as was the egg number function

$e(x, d = 780 \text{ km})$ of the offspring function. The mean length function (Table S1) reacted to a change in the slope parameter b_g quite strongly. With a 10 % reduction in the slope b_g of the mean length μ_g (Table S1), the cod would start to shrink at a length of around 78 cm. Thus, this was restricted for this modification in the function, and the cod was assumed not to grow to a new length the next year if $x > 78 \text{ cm}$. With those new vital rate functions, we

reanalysed the model with one change in the parameters at a time, following the steps as described in the main text.

In addition, a sensitivity analysis was conducted to further test the robustness of the model. We followed the approach by Vindenes et al. (2014), with their published R code. We tested the sensitivity of λ to current length x to understand how the different vital rates are affected by a small change in length by 0.1 %.

Results of robustness analyses

The robustness analysis of the model results showed that changes from $\pm 10\%$ in the parameters of the functions affect the numerical results obtained from the original model (Figure S3; main text Figure 4). However, even for the changes having the strongest effects, qualitative results within respect to the mean offspring length remained largely the same (Figure S3; main text Figure 3d, Figure 4), supporting the main conclusion of our study. The pattern of increased mean offspring length with migration distance was quite stable with regard to the changes in the survival parameter and egg numbers (Figure S3; main text Figure 4a, c). However, the changes in the mean growth slope b_g (Table S1) led to stronger effects on the model results. This was because the mean growth rate $\mu_g(x) - x$ changed quite drastically. The reduction of b_g by 10 % led to the necessary changes to restrict the length to the length from the year before (no further growing for fish > 78 cm). This led to stronger changes in λ , than for the other modifications of the parameters, leading to a stronger scaling to obtain the baseline $\lambda = 1$ for the Lofoten spawning ground, which was then followed by stronger mean offspring length μ_{L_1} changes than seen in the original model run (main text Figure 3d, Figure 4b). If the original model would have had this growth function, leading to unreasonable scaling of the egg survival to obtain $\lambda = 1$, we would have used a different modelling approach than the one we used now.

The sensitivity analysis of λ with respect to current length x indicated that the dynamics are highly affected by the vital rates in the small length classes (age 1). A slight increase in current length x in fish < 20 cm had strong impacts on their survival and growth which affected their respective contribution and thus led to positive impacts on λ (Figure S4; main text Figure 2a, b). In fish > 20 cm, a change in current length x caused survival to contribute positively to λ , however fish > 30 cm were negatively affected by increase in length, because of the onset of fishing mortality making the contribution of survival to λ slightly negative (Figure S4; main text Figure 2a). Growth was always contributing positively to λ , due to the increases from fecundity with larger length (Figure S4; main text Figure 2b, c). With the onset of maturity (fish > 50 cm), fecundity contributed positively to λ . For the largest lengths, the proportion of individuals in the model was so low that the contributions of their vital rates to the sensitivity approaches 0 (Figure S4). Since the offspring length distribution $L_1(y, d)$ is independent from maternal length x , the contribution to λ by a change in x is always zero, thus the offspring length contribution was not modelled here.

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Table S1 Fitted parameters for vital rates used in the baseline model

Vital rate	Parameter	Value
Survival $S(x)$	Slope a_s	0.2608
	Inflection point b_s (cm)	18.6276
	Slope c_s	0.0312
	Inflection point d_s (cm)	69.3121
Mean growth $\mu_g(x)$ of next year's length distribution $G(y; x)$	Intercept a_g	10.6068
	Slope b_g	0.9601
Next year's length distribution $G(y; x)$ standard deviation	σ_g (cm)	2
Offspring numbers $O(x, d)$	First year survival s_{first}	$7.1917 \cdot 10^{-5}$
	Probability of maturity $pm(x)$	
	Slope a_{mat}	0.1400
	Inflection point b_{mat} (cm)	69.8519
	Egg numbers $d = 780$ km	$e^{-15.09+3.595 \ln(x)}$
Offspring length distribution $L_1(y, d = 780$ km)	Mean μ_{L_1} (cm)	12.79
	Standard deviation σ_{L_1} (cm)	2

Table S2 Equations used for the energetic calculations for the spawning migration of NEA cod in the IPM model, equations based on Jørgensen and Fiksen (2006) including the number (No.) as they are mentioned in the text. The parameter values are found in Table S3.

Function	Equation	No.
Maximum energy storage (J)	$E_{max}(x) = (K_{max} - K_{min}) \frac{\rho_E \cdot x^{3+\varepsilon}}{100 \cdot L_{std}^\varepsilon}$	(1)
Somatic weight (grams wet weight)	$W_{soma}(x) = \frac{K_{min} \cdot x^{3+\varepsilon}}{100 \cdot L_{std}^\varepsilon}$	(2)
Total body mass (grams wet weight)	$W(x) = W_{soma}(x) + \frac{E_{max}(x)}{\rho_E}$	(3)
Standard monthly metabolic rate (J·month ⁻¹)	$SMR(x) = \frac{2166 \cdot W(x)^{0.828}}{Act_{std}}$	(4)
Duration of migration (days)	$T_M(d) = \frac{d}{U_S \pm U_C}$	(5)
Energy costs of migration (J)	$E_M(x, d) = SMR(x) \left[\left(\frac{\kappa_4 \cdot U_S^{1.5}}{x} + 1 \right) - Act_{std} \right] T_M(d)$	(6)

Table S3 Parameter values for NEA cod (Jørgensen & Fiksen 2006) for energetic equations in Table S2.

Parameter	Description	Value and unit
K_{max}	Maximum condition factor at standard length L_{std}	$1.25 \text{ g} \cdot \text{cm}^{-3}$
K_{min}	Minimum condition factor at standard length L_{std}	$0.75 \text{ g} \cdot \text{cm}^{-3}$
L_{std}	Length for which K_{min} is defined	70 cm
ε	Value of coefficient above 3 for allometric scaling between body mass and length	0.065
ρ_E	Energy density of muscle and liver energy stores	$8700 \text{ J} \cdot \text{g}^{-1}$
Act_{std}	Proportional increase in metabolic rate with activity	1.25
U_S	Swimming speed during spawning migration	$0.3 \text{ m} \cdot \text{s}^{-1}$
U_C	Speed of northwards currents	$0.1 \text{ m} \cdot \text{s}^{-1}$
κ_4	Coefficient for empirical cost of swimming function	$320 \text{ cm} \cdot \text{s}^{1.5} \cdot \text{m}^{-1.5}$

Figures

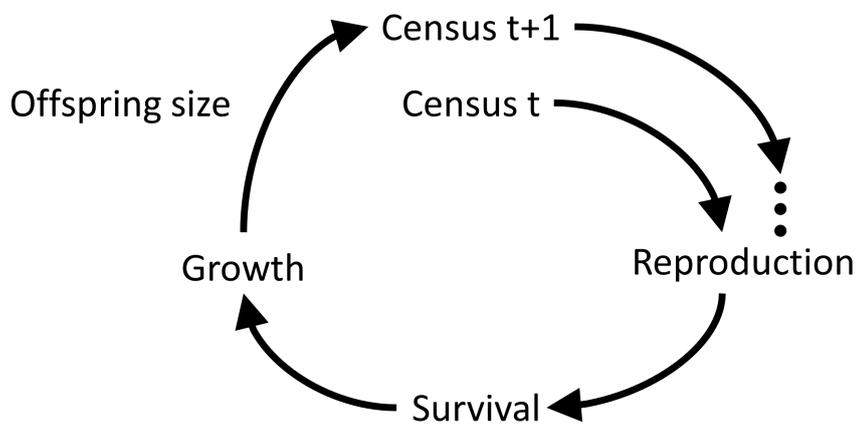


Figure S1. Schematic overview of life cycle diagram and life history events used for the IPM model of this study.

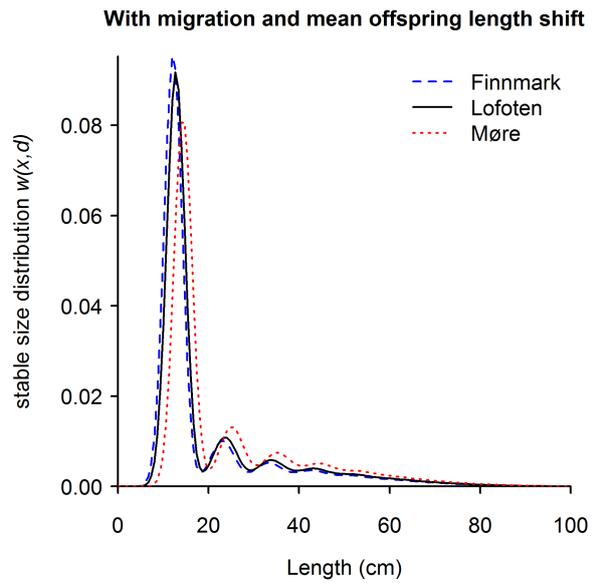


Figure S2. Stable size distribution of fish that migrated to Finnmark (blue dashed line), Møre (red dotted line) and Lofoten (black continuous line). We display the size distribution from $x = 0$ cm to $x = 100$ cm due to very small densities for sizes $x > 100$ cm.

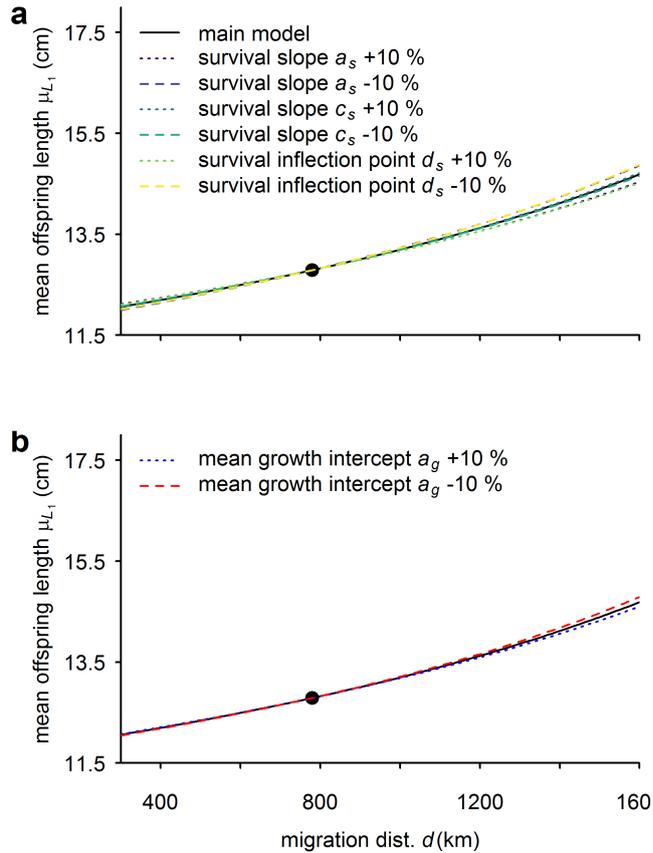


Figure S3. Changes in mean offspring length μ_{L_1} over the migration distance with alteration of vital rate parameters showing robustness of results. Here the parameters apart from the parameters leading to maximum change are presented (for maximum change, see main text Figure 4). The black line indicates the results from the model run without parameter changes. The black dot indicates where the Lofoten spawning ground lies a) Survival parameters slope a_s , slope c_s and inflection point d_s (Table S1) are perturbed by $\pm 10\%$. b) Mean growth parameter intercept a_g (Table S1) is perturbed by $\pm 10\%$.

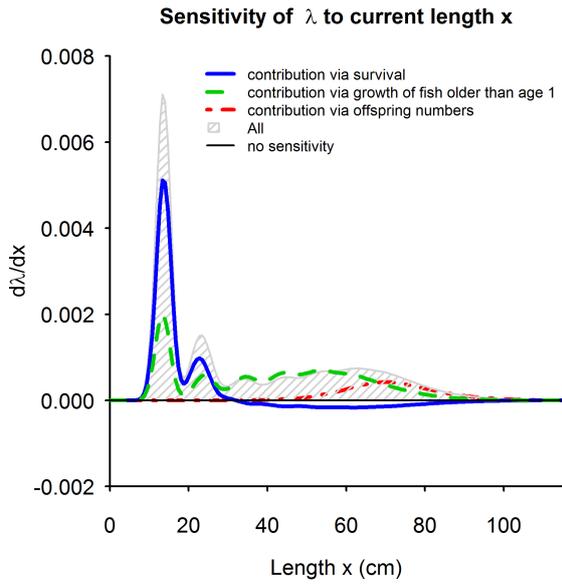


Figure S4. Sensitivity of λ to current length x decomposed into respective contributions of the vital rates survival $S(x)$, growth for fish older than age 1 $G(y; x)$, and offspring numbers $O(x, d)$.