

Supporting information for:

Low marine food levels mitigate high migration costs in anadromous populations

This supplementary note presents a detailed population-level model based on the individual life history described in the methods section of the main text. It also presents evidence and theory supporting two essential assumptions of the model: 1) the habitat switch to higher food levels results in larger and leaner individuals, 2) large individuals spend disproportionately more energy than small ones transporting their body upstream. Likewise, we show the effect of a nonlinear scaling of the costs of the breeding migration with respect to structural mass and of including the reversible mass in the costs of the breeding migration.

Physiologically-structured population model

The physiologically structured population model follows the approach introduced by Persson et al.(1) for populations with seasonal reproduction, in which the population is represented by a dynamic set of cohorts or year classes. Since reproduction occurs as a discrete event at a specific time in the year, all individuals that are born in the same reproductive event are considered equal and hence lumped into a single cohort and assumed to grow at the same rate. Thus, we can describe the dynamics of each cohort $i \in \mathbb{N}$ by using a system of ordinary differential equations, which keeps track of the density of individuals N_i , their age A_i , their structural mass W_i and their reversible mass S_i . Juveniles are defined as individuals with structural mass smaller than the structural mass at maturity W_p and adults as individuals with structural mass equal or larger than W_p . For each cohort i , age is monotonically increasing with time,

$$\frac{d}{dt}A_i = 1$$

(1)

The age of the individuals determines the stage, which in turn, determines the differential equations that describe the variation in density of individuals, their structural mass and stored

energy reserves. Equations (2), (3) and (4) below define the dynamics of eggs, presmolts and postsmolts respectively. The number of individuals decreases due to a mortality rate specific to each stage. In addition, the presmolts and postsmolts may die due to starvation. During the egg stage the structural mass and storage does not change. The dynamics of the structural and reversible mass in presmolts and postsmolts depend on the amount of food they encounter as well as the breeding migration period if they are adults.

for $0 \leq A_i < a_h$

$$\begin{cases} \frac{d}{dt} N_i = -\mu_e N_i \\ \frac{d}{dt} W_i = 0 \\ \frac{d}{dt} S_i = 0 \end{cases}$$

(2)

for $a_h \leq A_i < a_s$

$$\begin{cases} \frac{d}{dt} N_i = \begin{cases} -\mu_r N_i & \text{if } \frac{S_i}{W_i} \geq q_s \\ -\left(\mu_r N_i + \varphi \left(q_s \frac{W_i}{S_i} - 1\right)\right) & \text{if } S_i > 0 \text{ and } \frac{S_i}{W_i} < q_s \\ -\infty & \text{otherwise} \end{cases} \\ \frac{d}{dt} W_i = \begin{cases} \zeta_w \left(\kappa \frac{R_r}{K + R_r} j_a W_i^{2/3} - j_m W_i\right) & \text{if } \kappa \frac{R_r}{K + R_r} j_a W_i^{2/3} > j_m W_i \\ 0 & \text{otherwise} \end{cases} \\ \frac{d}{dt} S_i = \begin{cases} (1 - \kappa) \frac{R_r}{K + R_r} j_a W_i^{2/3} & \text{if } \kappa \frac{R_r}{K + R_r} j_a W_i^{2/3} > j_m W_i \\ \frac{R_r}{K + R_r} j_a W_i^{2/3} - j_m W_i & \text{otherwise} \end{cases} \end{cases}$$

for $a_s \leq A_i$

$$\left\{ \begin{array}{l} \frac{d}{dt} N_i = \begin{cases} -\mu_s N_i & \text{if } \frac{S_i}{W_i} \geq q_s \\ -\left(\mu_s N_i + \varphi \left(q_s \frac{W_i}{S_i} - 1 \right) \right) & \text{if } S_i > 0 \text{ and } \frac{S_i}{W_i} < q_s \\ -\infty & \text{otherwise} \end{cases} \\ \frac{d}{dt} W_i = \begin{cases} \zeta_w \left(\kappa f_s j_a W_i^{2/3} - j_m W_i \right) & \text{if } c1 \text{ and } (\sim c2 \text{ or } \sim c3) \\ 0 & \text{otherwise} \end{cases} \\ \frac{d}{dt} S_i = \begin{cases} (1 - \kappa) f_s j_a W_i^{2/3} & \text{if } c1 \text{ and } (\sim c2 \text{ or } \sim c3) \\ f_s j_a W_i^{2/3} - j_m W_i & \text{if } \sim c1 \text{ and } (\sim c2 \text{ or } \sim c3) \\ -(j_m W_i + C j'_m W_i^{PW}) & \text{otherwise} \end{cases} \end{array} \right.$$

(4)

In this last equation $c1$, $c2$ and $c3$ represent the conditions $\kappa f_s j_a W_i^{2/3} > j_m W_i$, $t_{um} \leq t \leq t_{dm}$, and $W_p \leq W_i$ respectively, while $\sim c1$, $\sim c2$ and $\sim c3$ refer to the situation that these conditions do not hold. When the conditions are true, the κ fraction of the amount of assimilates necessary is sufficient to meet metabolic maintenance ($c1$), the current time corresponds to the breeding migration period ($c2$) and the cohort is adult ($c3$).

Whenever a juvenile cohort reaches the maturation size $W_i = W_p$, at a particular time $t = t_p$, a maturation event occurs. At a maturation event, the juvenile cohort becomes an adult cohort.

This does not affect any cohort statistics:

$$\left\{ \begin{array}{l} A_i(t_p) = A_i(t_p^-) \\ N_i(t_p) = N_i(t_p^-) \\ W_i(t_p) = W_i(t_p^-) \\ S_i(t_p) = S_i(t_p^-) \end{array} \right.$$

(5)

Reproduction occurs instantaneously at $t = n t_y + t_r$, where $n \in \mathbb{N}$. At a reproductive event, a new cohort is formed from the reversible biomass of adults, if their reversible:structural mass ratio exceeds the reversible:structural mass ratio with which the adults matured:

$$\left\{ \begin{array}{l} A_0(t_{rn}) = 0 \\ N_0(t_{rn}) = \left(\sum_{i \in \{j \leq n | W_j \geq W_p\}} N_i \cdot \max \left(S_i - \frac{S_p}{W_p} W_i, 0 \right) \right) \frac{\zeta_e}{W_e} \\ W_0(t_{rn}) = \kappa W_b \\ S_0(t_{rn}) = (1 - \kappa) W_b \end{array} \right. \quad (6)$$

At the same time, all other cohorts are renumbered and the reversible mass of the reproducing adults is set to the amount that makes their reversible:structural mass ratio equal to their reversible:structural mass ratio at maturation.

$$\left\{ \begin{array}{l} A_{i+1}(t_{rn}) = A_i(t_{rn}^-) \\ N_{i+1}(t_{rn}) = N_i(t_{rn}^-) \\ W_{i+1}(t_{rn}) = W_i(t_{rn}^-) \\ S_{i+1}(t_{rn}) = \begin{cases} \min \left(S_i(t_{rn}^-), \frac{S_p}{W_p} W_i(t_{rn}^-) \right) & \text{if } W_i \geq W_p \\ S_i(t_{rn}^-) & \text{otherwise} \end{cases} \end{array} \right. \quad (7)$$

The resource density in the breeding habitat grows following a semi-chemostat growth and declines by foraging of presmolts (8).

$$\frac{d}{dt} R_r = \rho(R_{max} - R_r) - \frac{R_r}{K + R_r} j_a \sum_{i \in \{j \leq n | a_h < a_j < a_s\}} N_i W_i^{2/3} \quad (8)$$

Energy allocation effects of the habitat switch explained by dynamic energy budget theory

Dynamic energy budget (DEB) theory provides a conceptual framework to describe the individual life history based on individual energetic dynamics. DEB theory describes the rules by which an individual assimilates energy and utilizes it to grow, reproduce and cover metabolic maintenance (2–4). It has been used to describe the life history of several species including salmonids (5). In particular, the net assimilation model offers a conceptual explanation for the negative effect on fecundity caused by an increase in food abundance. This model assumes that a fraction κ of assimilates is allocated to first meet metabolic maintenance with the remainder of this fraction allocated to growth in structural mass, while a fraction $1 - \kappa$ is allocated to growth in reversible mass to be used for reproduction (Fig S1a) and covering energetic deficits during starvation periods. Given the assumption that metabolic maintenance is deducted from the fraction κ , a change in the proportion of assimilates required to meet metabolic maintenance affects the proportion of assimilates allocated to growth in structural mass but not the fraction allocated to growth in reversible mass. When an individual experiences a step-up change in food, the amount of assimilates available for growth, reproduction and metabolic maintenance increases. However, the amount of assimilates required to meet metabolic maintenance remains constant because the somatic structure of the individual does not suddenly change. Since the amount of total assimilates increases, the proportion of assimilates to meet metabolic maintenance thus decreases with the surplus now being allocated to growth in structural mass. Therefore, the proportion of assimilates allocated to growth in structural mass increases, while the proportion of assimilates allocated to growth in reversible mass, and thus to reproduction remains constant (Fig S1b). The model hence predicts that an individual that experiences a step-up change in food has lower energy density (lower ratio of reversible to structural mass) and consequently, lower mass-specific fecundity than an individual of the same size that never experiences a change in food, in line with data presented in Fig 1. Furthermore, the model predicts that this bias toward increased growth in structural mass compared to reversible mass is larger in individuals experiencing a large step-up change in food than in those experiencing a small one. Consequently, individuals that experience a large change in food grow larger (are bigger) and have a lower energy density (are leaner).

1 *Size-scaling of the breeding migration costs with structural mass and breeding migration*
2 *costs dependent on structural and reversible mass*

3 Metabolic rates of swimming and resting salmon scale with body mass with a power 0.79 and
4 0.78, respectively (6). It is important to notice that these exponents hold for an allometric
5 relation between metabolism and body mass, which quantities are different from the
6 metabolic maintenance and structural mass in the model that correspond to only part of the
7 metabolism and part of the body mass, respectively. However, this study suggests that
8 metabolic costs of swimming scale with a similar factor than resting metabolic costs.
9 Nonetheless, this study is based on fish swimming in still water but for swimming against a
10 current the energetic costs are different because the optimal speed is higher in the latter than
11 in the former (6).

12 The breeding migration entails multiple costs. In the freshwater habitat where the habitat is
13 not iso-osmotic, individuals invest energy in osmoregulation, such that respiration rate can
14 increase more than 20% just due to osmoregulatory expenses (7). These osmoregulatory
15 costs increase in proportion to the surface area of individual (3) and therefore scale
16 allometrically with the structural mass W with an exponent equal to 0.67. In addition, large
17 fishes travel upstream using portions of the river further from the bank than small ones (8)
18 where the current is faster and therefore they spend more energy traveling against a faster
19 current (9). In support of these arguments, data of energy expenditure during the breeding
20 migration of Chinook salmon *Oncorhynchus tshawytscha* show that the size-specific energy
21 requirements of large individuals are larger than of small individuals (10). That is, larger
22 individuals spend more energy per unit of structural mass than smaller ones (Fig S2), hence
23 PW is larger than 1. The energy loss during the migratory travel is also higher in large than in
24 small individuals of Atlantic salmon (11) and American Shad (*Alosa sapidissima*) (12).

25 Given this, we evaluated the effect that different size-scaling exponents of the costs of the
26 breeding migration PW have on population persistence (Fig S3). Smaller values of PW
27 increase persistence when costs of the breeding migration are high, because reversible mass
28 is depleted to a lesser extent during the breeding migration. Persistence of a migratory
29 population at low food levels but extinction occurring for higher food levels in the ocean when

30 the costs of the breeding migration are high occurs when PW is 0.5 or larger. This effect is
31 reversed for smaller PW , for example when equal to 0.3. However, the evidence presented
32 above makes values of PW below 0.5 unlikely and suggests that it actually scales with a
33 value larger than 1 with respect to body size, resulting in a stronger persistence effect of
34 declining food in the ocean when a population faces high costs of the breeding migration
35 because large individuals have higher size-specific migration costs than small individuals.
36 Based on that evidence, a choice of the size-scaling exponent of the energetic costs of the
37 breeding migration PW equal to 1 with respect to the structural mass as used in Fig 2 and 3 is
38 conservative. Our assumption of a size-scaling exponent of the energetic costs of the
39 breeding migration PW of 1 implies that structural mass-specific energetic costs of the
40 breeding migration are the same for every individual regardless of their body size, while
41 energetic costs of the breeding migration per unit of total mass (structural plus reversible)
42 decrease with body size because the reversible mass increases with body size (Fig S4).

43 An increasing impact of reversible mass on the costs of breeding migration, meaning taking
44 into account the total body mass in these costs, has no qualitative effects for the increase of
45 persistence of a migratory population at low food levels but extinction occurring for higher
46 food levels in the ocean when the costs of the breeding migration are high. However, the
47 costs of the breeding migration at which this phenomenon occurs are lower compared to the
48 case in which the costs of the breeding migration are independent of the reversible mass.
49 When the costs of the breeding migration are proportional to structural mass only the
50 population shows a small variation in the population biomass when the decrease of food level
51 in the ocean occurs in year 20, whereas when the costs of the breeding migration are
52 proportional to total mass (structural plus reversible) the population increases in biomass in
53 response to the decrease of food level (Fig S5). Therefore, including the reversible mass in
54 the costs of the breeding migration causes the population experiencing high food levels in the
55 ocean to go extinct at lower costs of the breeding migration but still to persist at low food
56 levels in the ocean.

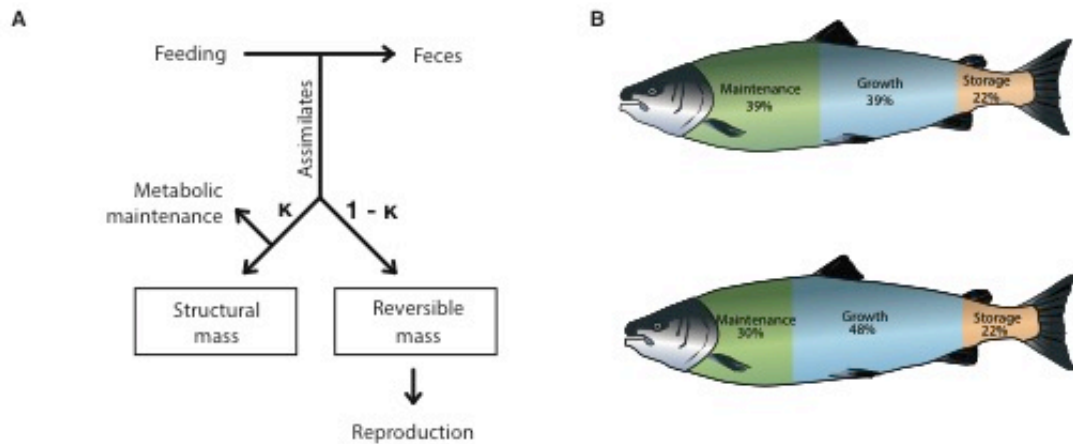


Figure S1. Energy allocation rule causes bias toward somatic growth after a large step-up change in food

57 **A:** Net assimilation energy budget model. When a step-up change in food occurs, metabolic
 58 maintenance requirements remain constant because the somatic structure only changes after
 59 growth has occurred. Because a fixed fraction κ of assimilates is allocated to cover both
 60 metabolic maintenance requirements and growth in structural mass, the sudden increase in
 61 available assimilates translates into a proportionally larger increase in the allocation to growth
 62 in structural mass compared to the increase in reversible mass. **B:** Proportion of assimilates
 63 allocated to growth (in structural mass), storage (reversible mass) and metabolic maintenance
 64 of individuals exposed to either a small (feeding level changes from 50 to 60% of maximum
 65 food intake; top) or large step-up in food abundance when switching habitats (feeding level
 66 changes from 50 to 90% of maximum food intake; bottom). See also Fig 2 and energy
 67 allocation effects of the habitat switch explained by dynamic energy budget theory.

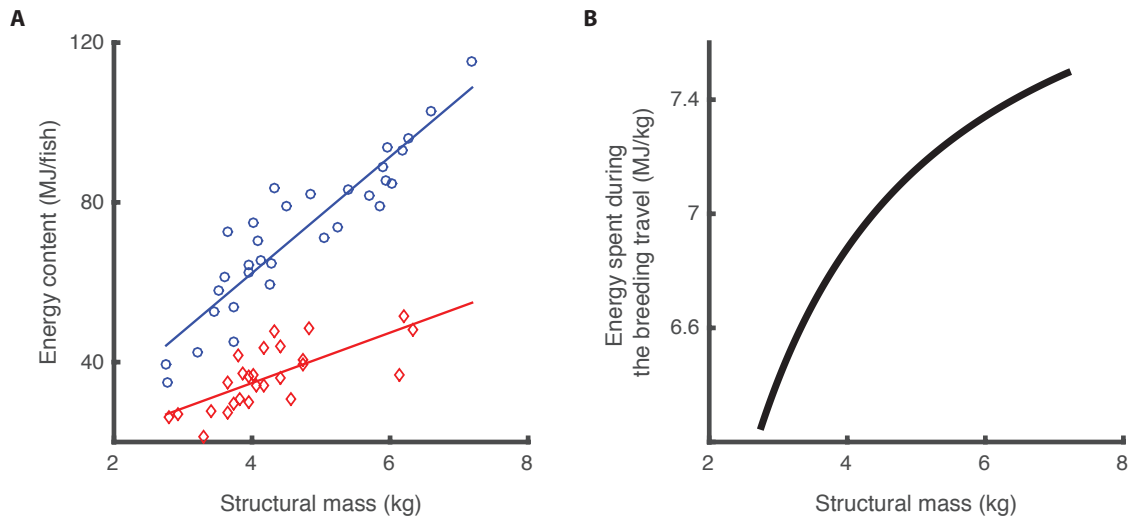
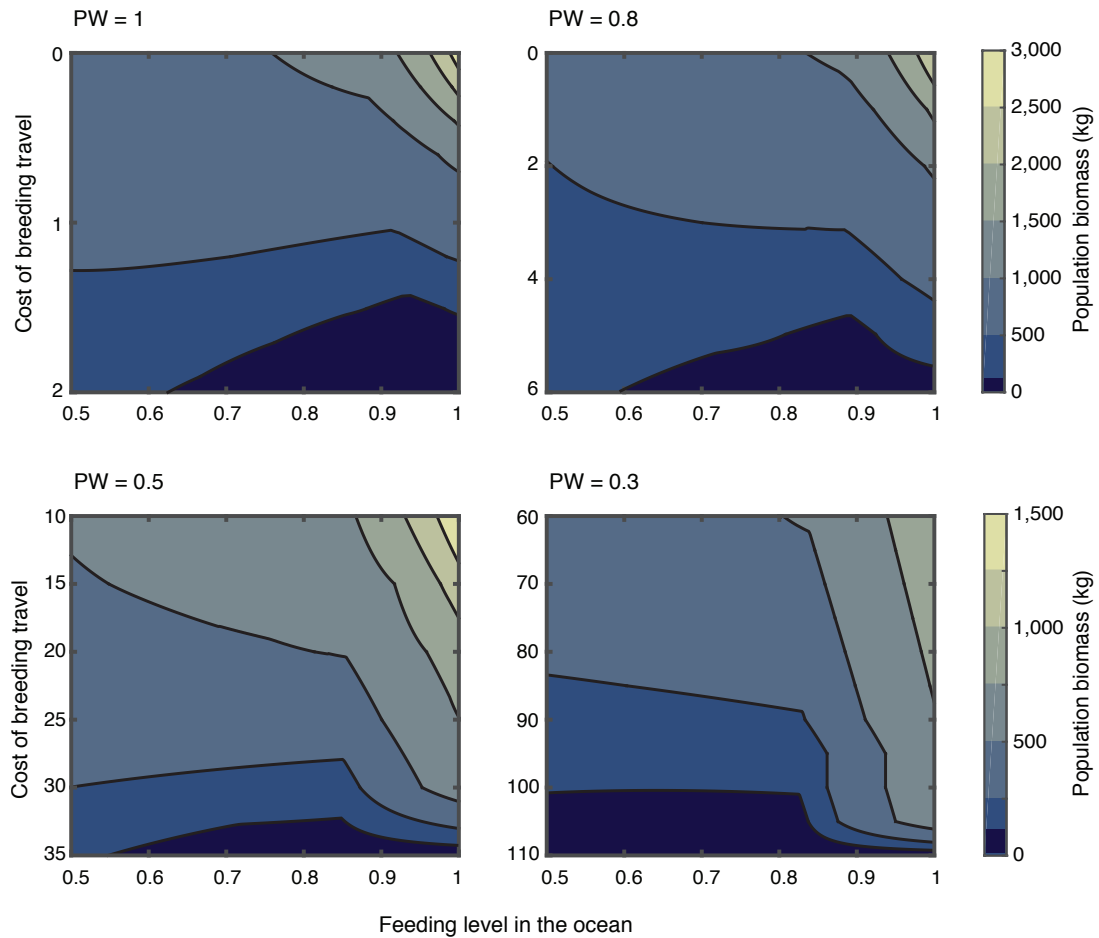


Figure S2. Title: Nonlinear scaling of the costs of the breeding travel with size in wild sockeye salmon

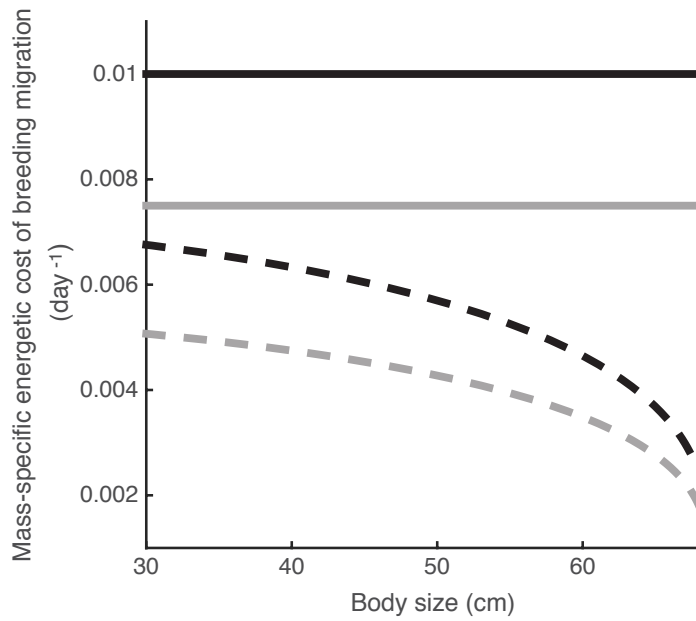
68 **A:** Total energy content of female individuals of *Onchorhynchus tshawytscha* at the beginning
 69 of the breeding travel ($E_{bt} = 14.57 \text{ Structural mass} + 4.0085$, R-squared = 0.845, blue) and at
 70 arrival in the spawning grounds ($E_{at} = 6.3057 \text{ Structural mass} + 9.5457$, R-squared = 0.514,
 71 red) from Bowerman et al(10) (data courteously provided by T. Bowerman). Structural mass
 72 was calculated from fork length Lf data ($\text{Structural mass} = dw (Lf * sc)^3$, where $dw =$
 73 1 g cm^{-3} is the density of the organism and $sc = 0.2$ is the shape coefficient for this species
 74 (5). **B:** Mass-specific energy expenditure calculated as the difference between the total
 75 energy content at the beginning of the breeding travel and at arrival in spawning grounds, and
 76 divided by the structural mass ($\text{Mass_specific energy spent during the breeding travel} = 8.26 -$
 77 $5.54 (\text{somatic mass}^{-1})$). See also Size-scaling of the breeding migration costs with structural
 78 mass and breeding migration costs dependent on structural and reversible mass.
 79



80

Figure S3. Consequences of interacting threats for population biomass with nonlinear scaling of the costs of the breeding travel with body size

81 Predicted biomass of anadromous populations exposed to different feeding levels in the
 82 ocean (horizontal axes) and facing different costs of the breeding travel (vertical axes) for four
 83 different scaling exponents of the costs of the breeding travel with individual body size. A
 84 population is considered to be extinct when its biomass is smaller than 100 kg (dark blue).
 85 Values shown represent the average population biomass computed over the stable annual
 86 cycle that the populations exhibit. See also Size-scaling of the breeding migration costs with
 87 structural mass and breeding migration costs dependent on structural and reversible mass.



88

Figure S4. Mass-specific costs of the breeding migration when this energetic costs scales with a factor of 1 with respect to structural mass ($PW = 1$) and the relative costs of the breeding migration are 0.5 ($C = 0.5$, grey lines) and 1 ($C = 1$, black lines).

89 For this factor, the energetic cost of the breeding migration divided by structural mass is the
 90 same for every individual regardless of its body size (solid lines), while the energetic cost of
 91 the breeding migration divided by its total body mass (structural mass + reversible mass)
 92 decreases with body size because reversible mass increases with body size. Data are
 93 representative for an individual migrating to the breeding grounds for first time after a feeding
 94 level of 0.6 in the ocean ($f_s = 0.6$).

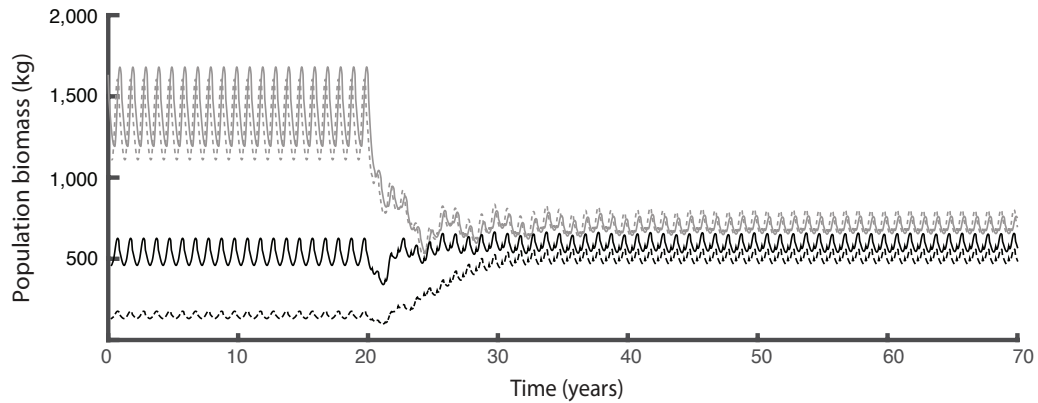


Figure S5. Population consequences of declining food abundance in the ocean when migration costs are dependent on total mass (structural plus reversible)

95 Biomass dynamics of a population facing low (0.5 times the normal field metabolic costs;
 96 grey) and high (1 times the normal field metabolic costs; black) costs of the breeding travel
 97 preceding and following a drop in feeding level in the ocean (as in Fig 2). Solid lines show
 98 dynamics for the default case (eq. 12) and dotted lines show the dynamics when the costs of
 99 the breeding travel dependent on total (structural plus reversible) mass (eq. 15). Notice that in
 100 the latter case the increase of population biomass when decreasing food levels in the ocean
 101 occurs at lower energy costs than in the former (Fig 2). See also Size-scaling of the breeding
 102 migration costs with structural mass and breeding migration costs dependent on structural
 103 and reversible mass.

104 **Table S1.** Summary of results of compensatory growth studies that reported fecundity

Species	Growth	Reduced fecundity due to step-up change?	Average individual fecundity		Units	Reference
			After step-up change in food	Control		
<i>Daphnia magna</i> (Cladoceran)	Indeterminate	Yes	15.1 *	60.1 *	eggs	(Kooijman, unpublished)
<i>Poecilia reticulata</i> (Fish)	Indeterminate	Yes	40.6 *	52.3 *	eggs	(13)
<i>Phalloptycus januarius</i> (Fish)	Indeterminate	Yes	4.5 *	7.5 *	eggs/week	(14)
<i>Uta stansburiana</i> (Lizard)	Indeterminate	Yes	3.53 *	5.1 *	eggs/clutch	(15)
<i>Aedes aegypti</i> (Insect)	Determinate	Yes	49 *	70 *	eggs	(16)
<i>Larinioides sclopetarius</i> (Arachnid)	Determinate	Yes	384 **	772 **	eggs	(17)
<i>Coturnix coturnix</i> (Bird)	Determinate	No				(18)
<i>Mus musculus</i> (Mammal)	Determinate	No				(19)

105

106 *Data digitalized from figures in the original publication

107 **Data listed in the original publication

108

Description	Symbol	Value	Unit	References
Environment				
Year	t_y	365	day	
Average temperature	T_m	283	K	
Amplitude of temperature variation	T_a	278	K	
Events within the season				
Day of the beginning of breeding travel	t_{um}	205		(20)
Day of reproduction (spawning)	t_r	215		(21)
Day of the end of breeding travel	t_{dm}	225		(20)
Age-dependent events during life cycle				
Age at hatching	a_h	150	day	(21,22)
Age at smolting	a_s	545	day	(23)
Food resource in the breeding habitat				
Resource growth rate	ρ	0.1	day ⁻¹	
Resource maximum density	R_{max}	5	g m ⁻³	
Half saturation resource density	K	1	g m ⁻³	
Migratory population				
Feeding level of postsmolts	f_s	varied	-	
Fraction of assimilation flux to structural mass growth and maintenance	κ	0.8		(5,24)
Maximum area-specific assimilation rate	j_a	0.18	g g ^{-2/3} day ⁻¹	Calculated with method of Jager (25) from regressions of Koskela et al (26)
Mass-specific metabolic maintenance costs	j_m	0.006	g g ⁻¹ day ⁻¹	Calculated with method of Jager (25) from regressions of Koskela et al (26)
Mass-specific metabolic costs of the breeding travel	j'_m	0.006	g g ^{-PW} day ⁻¹	
Reference temperature	T^*	293	K	
Arrhenius temperature	T_A	8000	K	
Yield of structural mass on assimilates	ζ_W	0.8	g g ⁻¹	(25)
Yield of egg buffer on reversible mass	ζ_e	0.95	g g ⁻¹	(25)
Mass of a single egg	W_e	0.1	g	(27)
Mass of a new born (after hatching)	W_b	0.06	g	(28)
Structural mass at maturity	W_p	74	g	(5)
Shape coefficient factor	δ	0.21	-	(5)
Density of structural mass	v	1	g cm ⁻³	
Costs of the breeding travel	C	varied	-	
Size scaling exponent of the costs of the breeding travel	PW	varied	-	
Mortality rate of eggs	μ_e	0.0125	day ⁻¹	(29)
Mortality rate of presmolts	μ_r	0.0025	day ⁻¹	(30)
Mortality rate of postsmolts	μ_s	varied	day ⁻¹	
Minimum reversible/structural mass ratio that individuals stand without starvation mortality	q_s	0.1	-	(1)
Scaling coefficient for starvation mortality	φ	0.2	-	(1)

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112

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