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RESEARCH ARTICLE

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Individual energy dynamics reveal nonlinear interaction of stressors threatening migratory fish populations

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Abstract

1. Migratory fish populations, like salmon, have dramatically declined for decades. Because of their extensive and energetically costly breeding migration, anadromous fish are sensitive to a variety of environmental stressors, in particular infrastructure building in freshwater streams that increases the energetic requirements of the breeding migration and food declines in the ocean.
2. While the effects of these stressors separately are well documented, the cumulative and interactive impacts of them are poorly understood.
3. Here, we use a bioenergetics model recently developed for fish life history to investigate the individual life history and population responses to these stressors combined.
4. We find that food decline in the ocean can mitigate rather than exacerbate the negative effect of elevated migration costs imposed by infrastructure building in streams. This counterintuitive effect results from the highly nonlinear manner in which these stressors interact and affect the individual energetics. In particular, this effect arises from the fact that individuals growing in the ocean under higher food conditions reach larger sizes with concomitant larger migration costs but are leaner. As a consequence of their lower energy densities, they spend most of their energy reserves to transport their body upstream when migration costs are high, and little is left for reproduction, resulting in lower individual fitness.
5. Our results highlight the need of a mechanistic understanding integrating individual energetics, life history and population dynamics to accurately assess biological consequences of environmental change.

KEYWORDS

anadromous population, breeding migration, individual energy budget, multiple stressors, population dynamics

1 | INTRODUCTION

Migratory fish populations have shown dramatic declines over the last decades. In the North Atlantic, historical records of 24 migratory fish species reveal that they all decreased in abundance by more than 90% (Limburg & Waldman, 2009). Conservation of these populations is of particular concern because of their economic and cultural importance: although anadromous fish comprise on average <1% of the world fish species, their share in global fisheries trade currently exceeds 17% and continues to increase (FAO, 2016). Anadromous fish are exposed to a wide range of environmental influences in both freshwater and marine habitats, which make them particularly vulnerable to environmental change. Multiple stressors have contributed to the decline of anadromous populations (Limburg & Waldman, 2009), including infrastructure

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building in freshwater streams and food declines in the ocean. In fact, collapse of Atlantic salmon *Salmo salar* populations throughout North-Western Europe in pre-modern times coincided with the spread of watermills in river basins (Lenders et al., 2016). Likewise, a multidecadal decline of food abundance in the ocean occurs concurrently with the reduction of Atlantic salmon abundance (Friedland et al., 2009).

On their own, food reductions in the ocean and infrastructure building in freshwater streams have negative impacts on fish life history by affecting individual energetics. Low food abundance in the ocean limits body growth rate during the oceanic stage resulting on average in individuals with smaller body sizes (Friedland et al., 2009) and concomitant lower fecundity (Thorpe et al., 1984). On the other hand, dams and other anthropogenic structures increase the energetic costs of the breeding migration (Caudill et al., 2007; Mesa & Magie, 2006). Significant numbers of adult salmonids passing dams can fall back over the dam or travel some distance in a fishway, but eventually fall out (Bjornn et al., 1999; Dauble & Mueller, 2000). In both instances, additional energy is required to re-ascend the dam. Individuals may also incur additional energetic costs due to prolonged migration at dams, which can be caused, for instance, by the need to find fishway entrances (Dauble & Mueller, 2000). Because individuals cease feeding when leaving the ocean and use only their stored energy reserves to meet the energetically costly upriver travel (Jonsson et al., 1997), this results in a depletion of energy reserves available for reproduction (Crossin et al., 2004). While the effects of food reduction in the ocean and increased migration costs separately are well documented, the cumulative and interactive impacts of them are poorly understood.

In this study, we assess the cumulative and interactive impact of high costs of the breeding migration and a decline in ocean food availability on the ecology of anadromous fish species. Specifically, we investigate how these stressors interact and affect individual energetics and thus the individual life history using a bioenergetic model for ontogenetic development based on energy allocation between growth, energy reserves and reproduction in fishes (Martin et al., 2017). We furthermore explore the population consequences of our individual-level findings.

2 | MATERIALS AND METHODS

We study the effects of high costs of the breeding migration and a decline in ocean food availability on the ecology of anadromous fish species. Using a bioenergetic model, we first investigate the effects of these stressors on the individual life history. Subsequently, we extend our analysis to explore how these life-history effects impact the population dynamics.

2.1 | Individual life history

2.1.1 | Bioenergetic model

The description of the individual energetic dynamics and its link with life history follows the bioenergetics approach introduced by Kooijman and Metz (1984) in which the energy allocation to somatic and reproductive metabolism is proportional to a fraction κ and a $1-\kappa$ of the total energy assimilation rate respectively. Specifically, we adopt the model developed and described in detail by Martin et al. (2017) for fish, because it provides an explicit dynamics of energy reserves (in our model referred to as reversible mass) that are necessary to model individual life history with starvation periods like those happening during the breeding migration. Here we provide only a concise synopsis of the model.

Individuals are characterized by three state variables: individual age A, structural mass W and reversible mass S. Age is a monotonically increasing function of time, $\mathrm{d}A/\mathrm{d}t = 1$. Structural mass we consider to include bones and organs which cannot be starved away to cover energetic demands, whereas reversible mass comprises stored energy reserves such as fat and gonads. The body mass of an individual is therefore the sum of its structural and reversible mass. Body length l and structural mass W are related to each other following:

$$W = v(\delta l)^3, \tag{1}$$

where v is the density of structural mass and δ is a shape coefficient factor.

The rate of energy assimilation is given by:

$$J_F = f j_a W^{\frac{2}{3}},$$

where f is the feeding level in either the breeding (f_r) or the non-breeding habitat (f_s), j_a is the maximum area-specific assimilation rate and the surface area for assimilation scales with the structural mass to the power of 2/3.

Metabolic maintenance costs are the product of the structural mass-specific maintenance costs j_m and the structural mass:

$$J_M = j_m W.$$

The linear scaling between metabolic maintenance costs and structural mass is broadly used in diverse formulations of energy allocation throughout growth and development for diverse organisms in general (e.g. Kooijman, 2010; Kooijman & Metz, 1984; Nisbet et al., 2000; West et al., 2001), and for salmonids in particular (Pecquerie et al., 2011). Notice that this assumption implies that increases in reversible mass during life history can lead to a sublinear scaling of maintenance costs with total body mass, which is the sum of structural and reversible mass.

Assimilates are assumed to split into a somatic and a reversible mass flux: the κ flux and the $1-\kappa$ flux. The somatic, κ flux is used to meet metabolic maintenance requirements first, while the remaining flux J_W is used to synthesize structural mass. In turn, the $1-\kappa$ flux J_S is allocated to reversible mass. Thus,

$$J_W = \left(\kappa J_F - J_M\right),$$

$$J_S = (1-\kappa) J_F.$$

If the metabolic maintenance costs are larger than the κ flux, the individual starves and stops growing. If the metabolic maintenance costs

are larger than the flux of assimilates, the individual depletes its reversible mass to cover the deficit in maintenance requirements:

$$J_W = 0,$$

$$J_S = J_F - J_M.$$

Therefore, the individual state dynamics are described by the following system of differential equations (Martin et al., 2017):

$$\frac{dW}{dA} = \begin{cases} \zeta_W \left(\kappa f j_a W^{\frac{2}{3}} - j_m W\right) & \text{if } \kappa f j_a W^{\frac{2}{3}} > j_m W \\ 0 & \text{otherwise} \end{cases}, \tag{2}$$

$$\frac{dS}{dA} = \begin{cases} (1-\kappa) f j_a W^{\frac{2}{3}} & \text{if } \kappa f j_a W^{\frac{2}{3}} > j_m W \\ f j_a W^{\frac{2}{3}} - j_m W & \text{otherwise} \end{cases}. \tag{3}$$

The parameter ζ_W in Equation (2) represents the efficiency with which assimilates are converted into structural mass.

Individuals mature when they reach a fixed structural mass W_p. Based on observations on a wide range of species that the average year to year energy density of mature fish does not systematically increase or decrease with body size in iteroparous species, Martin et al. (2017) adopted the reversible:structural mass ratio at maturity S_p/W_p as the threshold for reproductive investment. The surplus of reversible mass in excess of the amount that equals the S_p/W_p reversible:structural mass ratio is used for reproduction. Reproduction occurs at a discrete time t_r. The number of offspring θ produced by an adult individual with structural mass W and reversible mass S, hence, equals:

$$\theta = \left(S - \frac{S_p}{W_p} W\right) \frac{\zeta_e}{W_e}, \tag{4}$$

if $S/W > S_p/W_p$, and equals 0 otherwise. Notice that the above expression implies that fecundity is 0 for just maturing fish (for which $W = W_p$ and $S = S_p$) and increases with size afterward if food is abundant. If reproduction occurs, the reversible mass of reproducing individuals is simultaneously reduced to $S = (S_p/W_p)\, W$. The number of offspring produced is dependent on the yield for the conversion of reversible mass into eggs ζ_e and the egg mass W_e. During the egg stage individuals do not feed, therefore we assumed newly hatched individuals to be born at t_h with a structural mass equal to κW_b and a reversible mass $(1-\kappa)\, W_b$.

During the breeding migration the individuals cease feeding, stop growing and use their reversible mass to meet their metabolic maintenance costs and the costs of the travel, which is assumed to be an allometric function of the metabolic maintenance costs:

$$\frac{dS}{dA} = -\left(j_m W + C j'_m W^{\gamma}\right) \tag{5}$$

In Equation 5, the first term of the sum at the right-hand side corresponds to the basal metabolic costs, and the second term relates to the travelling costs of the breeding migration. C represents the relative costs of the breeding migration, j'_m is the structural mass-specific metabolic costs of the breeding migration and γ is the size-scaling exponent for the costs of the breeding migration. When $\gamma = 1$, structural mass-specific energetic costs of the breeding migration are the same for every individual regardless of their body size. However, when γ is smaller (larger) than 1, large individuals have lower (higher) structural mass-specific migration costs than small individuals.

Individuals may die from either starvation or background mortality. Individuals with an S/W ratio smaller than q_S experience increased mortality due to starvation, described by:

$$\mu_{\text{starving}} = \begin{cases} 0 & \frac{S}{W} > q_S \\ \varphi\left(q_S \frac{W}{S} - 1\right) & \text{if } S > 0 \text{ and } \frac{S}{W} \le q_S \\ \infty & \text{otherwise} \end{cases}, \tag{6}$$

where φ is a positive proportionality constant (Persson et al., 1998).

Once they have depleted their reversible mass entirely ($S = 0$), starving individuals die instantaneously.

In addition to starvation mortality, individuals die at a rate μ_e during the egg stage, at a rate μ_r if they are presmolts and μ_s if they are postsmolts. The total per capita death rate is the sum of the different sources of mortality.

2.1.2 | Yearly cycle and life-history events

Life-history parameters used in the model are based on the biology of Atlantic salmon *Salmo salar*. In this species, like in other anadromous species, the first life stages occur in the freshwater habitat where the parents breed. Female salmon spawn in autumn at time t_r, the eggs develop throughout winter and hatch at age a_h (in spring; Hendry & Cragg-Hine, 2003). After hatching, individuals remain in the stream until age a_s, when they smolt and migrate to the ocean (Hendry & Cragg-Hine, 2003; hereafter, individuals younger than a_s are referred to as presmolts, in contrast to older individuals that are referred to as postsmolts). Every autumn, all sexually mature individuals in the ocean return to the freshwater habitat and start migrating upstream at time t_{um} to spawn somewhat later at time t_r. After spawning, postsmolts finish downstream migration and return to the sea at time t_{dm} of the year.

2.1.3 | Habitats

During their early life stages in freshwater, anadromous individuals often experience strong density dependence and intense competition for food, while density dependence in the ocean is more relaxed and food is more abundant (Jonsson et al., 1998). As a consequence, individuals experience an increase in food availability during the switch from freshwater to seawater (MacFarlane, 2010). We thus

consider an increase in the feeding level during the habitat switch when analysing the individual dynamics, $f_s > f_r$.

We also explicitly account for density dependence in the breeding habitat when analysing the population dynamics. Because strong density dependence in early life stages directly affects growth in body size in salmonids (Walters et al., 2013), we incorporate density-dependent effects on the growth rate of presmolts via competition for food. In the absence of consumers, the food resource density in the breeding habitat, indicated with R_r, is assumed to follow a semi-chemostat growth dynamics with maximum density $R_{\max}$ and growth rate ρ (for an explanation and justification of this type of growth dynamics, see Persson et al., 1998):

$$\frac{\mathrm{d}R_r}{\mathrm{d}t} = \rho(R_{\max} - R_r). \tag{7}$$

Assuming that food consumption of presmolts follows a Holling type II functional response yields the following expression for the feeding level:

$$f_r = \frac{R_r}{K + R_r}, \tag{8}$$

where K is the half saturation food density.

In contrast, in the marine habitat, we assume a constant feeding level f_s as density dependence is negligible (Jonsson et al., 1998).

2.2 | Population dynamics

We use the model formulated by Chaparro-Pedraza and de Roos (2019) to describe the dynamics of anadromous populations based on individual energetic dynamics. Here we provide a synopsis of the model. In the model, individuals use two different habitats in different life stages and exploit a different resource in each habitat. The anadromous population is structured by age, structural and reversible mass and follows semi-discrete dynamics: continuous dynamics describe the resource consumption, growth in both structural and reversible mass and survival and a discrete map describes the pulse-wise reproduction. 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 lumped into a single cohort. Individuals in the same cohort are assumed to grow at the same rate. Hence, at the population level, we can describe the dynamics of every cohort by using a system of ordinary differential equations, which keeps track of the number of individuals, their age, structural and reversible mass (see Appendix S1). Therefore, the dynamics of the entire population can be followed by numerically integrating the ordinary differential equations for each cohort separately. When a reproductive event occurs, a new cohort is added to the population, which implies additional differential equations describing the population dynamics. In addition, changes in food density in the freshwater habitat can be followed by numerical integration of the ordinary differential equation that accounts for resource food growth and consumption. The numerical integration is carried out using the Escalator Boxcar Train (de Roos, 1988), a numerical integration method specifically designed to handle the system of differential equations that describe a physiologically structured population model.

2.3 | Model parameterization

Parameter values are based on the biology of Atlantic salmon (Table 1). Values for the parameters in the functions describing individual feeding, growth and reproduction are derived from the underlying parameters of the dynamic energy budget model (Martin et al., 2017). Values for the parameters representing life-history traits, such as body size at birth and age at smolting, were derived from reported data in the literature. Atlantic salmon are considered mature when they return to the streams to spawn (around a body length of 50 cm; Hutchings & Jones, 1998), however, at this point, individuals have already accumulated large amounts of energy for reproduction. It is unknown, however, when they start to allocate this energy to reproduction. In our model, individuals start to allocate energy to reproduction at the maturation threshold. We assume this threshold to be lower than the body length at which Atlantic salmon has been documented to return (20 cm). We assess the robustness of our results also for other values of the maturation threshold (see Section 2.4).

The energetic costs of the breeding migration depend on the parameters C, j'_m and γ. In this study we investigate the effects of, and hence vary, the relative costs of the breeding migration C. Therefore, in this section, we focus on the estimation of the values of j'_m, and γ. We assume the structural mass-specific metabolic costs of the breeding travel, j'_m, to be the same as the structural mass-specific metabolic maintenance costs, j_m. Concerning the value of γ, Alexander (1998) estimates that metabolic costs of swimming in still water scale sublinearly with respect to body mass, specifically with an exponent of 0.79. However, swimming upstream against a current entail different energetic costs because the optimal speed is higher in the latter than in the former (Alexander, 1998). In addition, during the breeding migration, large fish travel upstream using portions of the river further from the bank than small ones (Hughes, 2004), where the current is faster and therefore they spend more energy travelling against a faster current (Hinch & Rand, 2000). In support of these arguments, data of energy expenditure during the breeding migration of Chinook salmon *Oncorhynchus tshawytscha* show that larger individuals spent more energy per unit of structural mass than smaller ones and the energetic costs of the breeding migration scale superlinearly with structural mass (i.e. $\gamma > 1$; see Figure S1; Bowerman et al., 2017). Likewise, the percentage of energy spent during the migratory travel is higher in large than in small individuals of Atlantic salmon (Jonsson et al., 1997) and American Shad *Alosa sapidissima* (Glebe & Leggett, 1981). Taken together, this evidence suggests the energetic costs of the breeding migration to scale superlinearly with mass and thus $\gamma > 1$. We take a conservative approach by adopting a linear scaling of energetic costs of the breeding migration with

TABLE 1 Parameter values

Description	Symbol	Value	Unit	References
Environment				
Year	t_y	365	day	
Events within the season				
Day of the beginning of breeding travel	t_{um}	205	day	Doucett et al. (1999)
Day of reproduction (spawning)	t_r	215	day	Thorpe et al. (1998)
Day of the end of breeding travel	t_{dm}	225	day	Doucett et al. (1999)
Age-dependent events during life cycle				
Age at hatching	a_h	150	day	Hendry and Cragg-Hine (2003) and Thorpe et al. (1998)
Age at smolting	a_s	545	day	Mccormick et al. (1998)
Food resource in the breeding habitat				
Feeding level	f_r	0.4[a]	—	
Resource growth rate	ρ	0.01[b]	day^{-1}	
Resource maximum density	R_{max}	5[b]	g/m^3	
Half saturation resource density	K	1[b]	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		Pecquerie et al. (2011) and Jager et al. (2013)
Maximum area-specific assimilation rate	j_a	0.0572[c]	$g/g^{2/3}\ day^{-1}$	Calculated with method of Jager et al. (2013) from regressions of Koskela et al. (1997)
Mass-specific metabolic maintenance costs	j_m	0.0019[c]	$g/g\ day^{-1}$	Calculated with method of Jager (Jager et al., 2013) from regressions of Koskela et al. (1997)
Mass-specific metabolic costs of the breeding travel	j'_m	0.0019[c]	$g\ g^{-\gamma}\ day^{-1}$	
Yield of structural mass on assimilates	ζ_W	0.8	g/g	Jager et al. (2013)
Yield of egg buffer on reversible mass	ζ_e	0.95	g/g	Jager et al. (2013)
Mass of a single egg	W_e	0.1	g	Potts and Rudy (1969)
Mass of a new born (after hatching)	W_b	0.06	g	Shearer et al. (1994)
Structural mass at maturity	W_p	74	g	Pecquerie et al. (2011)
Reversible mass at maturity	S_p	—	g	
Shape coefficient factor	δ	0.21	—	Pecquerie et al. (2011)
Density of structural mass	v	1	g/cm^3	
Constant for the costs of the breeding migration	C	varied	—	
Structural mass-scaling exponent of the costs of the breeding migration	γ	1	—	
Mortality rate of eggs	μ_e	0.0125	day^{-1}	Bley and Moring (1988)
Mortality rate of presmolts	μ_r	0.0025	day^{-1}	Leggett and Power (1969)
Mortality rate of postsmolts	μ_s	0.0063	day^{-1}	Hutchings and Jones (1998)
Minimum reversible/structural mass ratio that individuals stand without starvation mortality	q_S	0.1	—	Persson et al. (1998)
Scaling coefficient for starvation mortality	φ	0.2	—	Persson et al. (1998)

[a]Used when investigating the individual life-history dynamics.

[b]Used when investigating the population effects of the individual life-history dynamics.

[c]The rate constant (j_a, j_m, j'_m) values include a temperature correction following the Arrhenius relationship for a temperature of 10°C.

structural mass, that is, $\gamma = 1$. It is important to bear in mind that when adopting $\gamma = 1$, the structural mass-specific energetic costs of the breeding migration are the same for every individual regardless of their body size. In the Supporting Information (Figures S3 and S4), however, we assess the robustness of our results when such costs scale sublinearly and superlinearly (see Section 2.4).

2.4 | Model analysis

We first investigate the fitness consequences of the cumulative and interactive impact of costs of the breeding migration and changes in ocean food availability. We compare the life-history trajectories of individuals growing under conditions of high and low food availability as well as high and low costs of the breeding migration (Figure 1). Specifically, we follow during the life history the structural mass, reversible mass, cumulative fecundity and expected reproductive output. We also evaluate how reversible mass changes during the breeding migration (Figure 2). We furthermore assess the cumulative and interactive impact of costs of the breeding migration and feeding level in the ocean on the individual fitness (i.e. lifetime reproductive output; Figure 3).

Subsequently, we investigate the population effects of the individual fitness consequences found in the previous step. We thus simulate a reduction in feeding level in the ocean in a population experiencing high and low costs of breeding migration. To do so, we compute the dynamics of the population biomass for 100 years exposed to low, $C = 1.5$, and high costs of the breeding migration, $C = 2.5$. During the first 20 years the feeding level in the ocean f_s was assumed high (0.8 times the amount of food ad libitum) whereas it was low during the following 80 years (0.5 times the amount of food ad libitum; Figure 4). We also evaluate the effects of costs of the breeding migration and feeding level in the ocean (between 0.5 times the amount of food ad libitum and food ad libitum) on the population biomass (Figure 5).

We evaluate the robustness of our results regarding changes in the maturation threshold. Specifically, we calculate the structural mass, reversible mass, cumulative fecundity and expected reproductive output under conditions of high and low food availability when

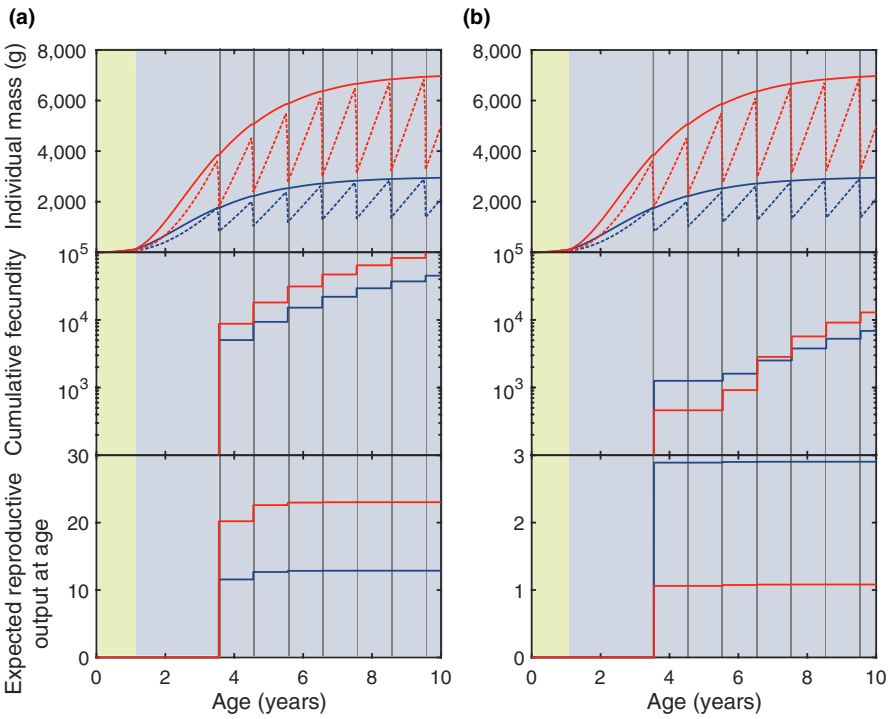

FIGURE 1 Fitness components as a function of age when costs of the breeding migration are (a) low and (b) high, and under conditions of high (red lines) and low (blue lines) food abundance in the ocean. Structural (solid line) and reversible mass (dashed lines) are shown in the top panels, cumulative fecundity in the middle panels and expected reproductive output in the bottom panels (notice that the vertical axes differ by one order of magnitude in a and b). Individuals start their life in the freshwater habitat (background yellow region), later they smolt and migrate to the ocean (background blue region). After reaching maturity, individuals migrate yearly back to the freshwater habitat to breed (background grey lines). Costs of migration C are 1 in (a) and 3 in (b). Feeding level in the ocean $f_s = 0.6$ when low and $f_s = 0.8$ when high. Other parameter values as in Table 1

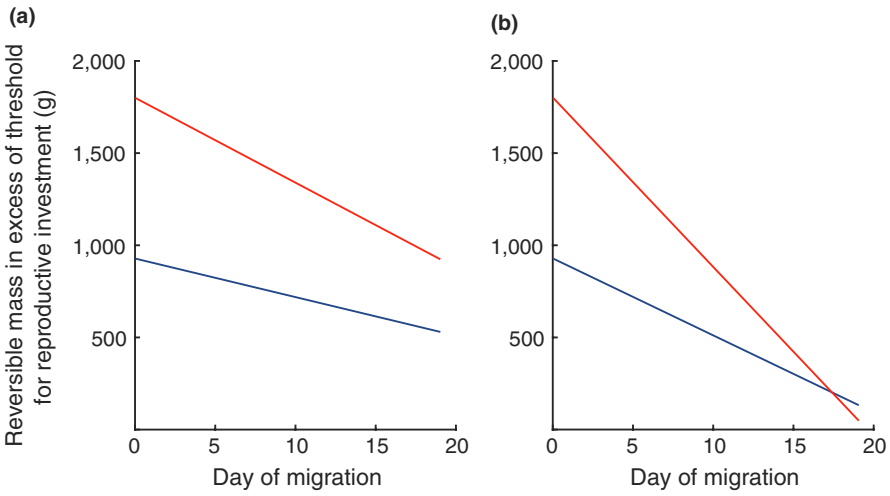

FIGURE 2 Changes in reversible mass during the first breeding migration when costs of migration C are (a) low and (b) high, and under conditions of high (red lines) and low (blue lines) food abundance in the ocean. Parameter values as in Figure 1

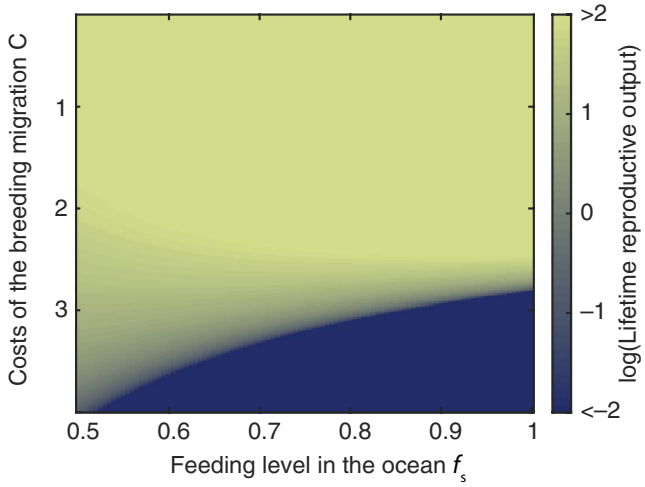

FIGURE 3 Lifetime reproductive output (colour scale) as a function of the costs of the breeding migration and the feeding level in the ocean. Other parameter values as in Table 1

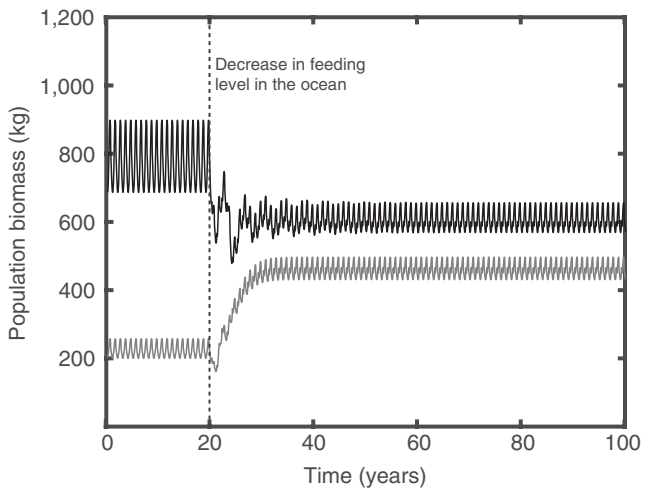

FIGURE 4 Population biomass dynamics when costs of the breeding migration are low (black line) and high (grey line). Feeding level in the ocean f_s is initially 0.8 times the amount of food ad libitum (time 0 to 20 years) and drops to 0.5 after year 20 (dashed line). Costs of the breeding migration C are 1.5 when low and 2.5 when high. Other parameter values as in Table 1

the costs of the breeding migration are high for individuals with a maturation threshold of 25 and 30 cm (Figure S2).

Additionally, we assess the robustness of the results regarding both, the individual fitness (Figure S3) and the population effects (Figure S4), of the interacting stressors under scenarios in which the energetic costs of the breeding migration scale sublinearly and superlinearly with respect to structural mass. Based on the estimation of the scaling of metabolic costs when swimming in still water made by Alexander (1998), we adopt $\gamma = 0.8$ for the sublinear scaling, and $\gamma = 1.2$ for the superlinear scaling. Because the energetic effects of the breeding migration depend on both the relative costs of the migration C (that scales linearly the parameter j'_m) and the size-scaling exponent of the costs of breeding migration

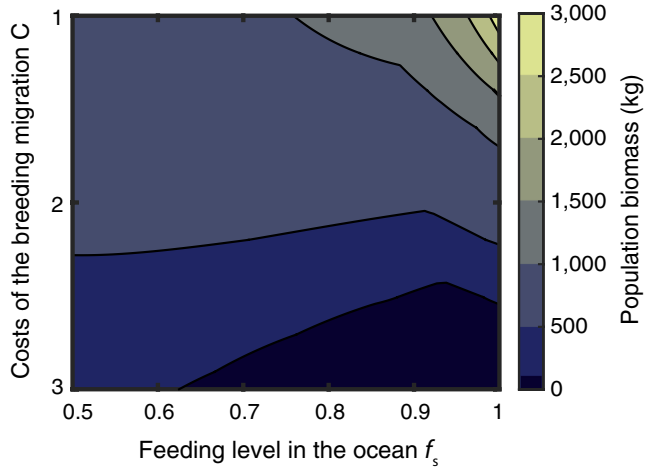

FIGURE 5 Population biomass (colour scale) as a function of costs of the breeding migration C and feeding level in the ocean f_s. Other parameter values as in Table 1. The values correspond to the average population biomass after the transient dynamics have disappeared

γ, the range of values explored in the parameter space of C varies with γ. Therefore, when investigating the population effects of a reduction in feeding level in the ocean (Figure S4), we adopt $C = 10$ and $C = 15$ for low and high costs of the breeding migration when $\gamma = 0.8$ and $C = 0.1$ and $C = 0.5$, when $\gamma = 1.2$. As in Figure 4, for this analysis we simulate a reduction in food abundance in the ocean in the year 20 (f_s drops from 0.8 to 0.5 times the amount of food ad libitum).

3 | RESULTS

3.1 | Individual life-history effects of costs of the breeding migration and changes in ocean food availability

As expected, high food abundance in the ocean results in high fitness (i.e. lifetime reproductive output) when an individual experiences low costs of the breeding migration (Figure 1a). But surprisingly, high food abundance in the ocean results in lower fitness when an individual experiences high costs of the breeding migration (Figure 1b). This result is robust to variation in the maturation threshold (see Figure S2). Under both scenarios of high and low costs of the breeding migration, the structural and reversible mass accumulate faster when feeding level in the ocean is high. Although the structural and reversible mass trajectories follow the same trajectories regardless of the costs of the breeding migration, the cumulative fecundity and expected reproductive output trajectories differ for different levels of costs of the breeding migration. When an individual experiences low costs of the breeding migration, its fecundity is higher at any age if food abundance in the ocean is high than if it is low. In contrast, when an individual experiences high costs of the breeding migration, its fecundity is lower in the first breeding migration if

food abundance in the ocean is high than if it is low. Nonetheless, in later breeding migrations the fecundity of such individual exposed to high food abundance in the ocean is higher than if food abundance is low. As a result, the total cumulative fecundity is higher when food abundance in the ocean is higher (see cumulative fecundity at age 10 years). Because survival decreases with age, the contribution of late reproductive events to the lifetime reproductive output is, however, low compared to early reproductive events. Therefore, when facing high costs of the breeding migration, an individual has higher fitness if it encounters low food abundance in the ocean because its fecundity is higher in the early reproductive events than a comparable individual that encounters high food abundance in the ocean.

The cause of the fecundity reduction in the early reproductive events with increasing food abundance in the ocean when costs of the migration are high lies in the depletion of reversible mass during the breeding migration. A large individual requires more energy to mobilize its body during the upstream migration. Since an individual in a rich feeding ocean grows faster but leaner than an individual in a poor feeding ocean, the depletion of reversible mass during the breeding migration is steeper in the large fast-growing individuals (Figure 2). When the costs of the migration are low, the energy consumption to fuel the breeding migration does not represent an important proportion of the energy available as reversible mass. However, when the breeding migration is energetically costly the depletion of reversible mass is dramatic and leads to a significant reduction of energy available for reproduction. The steeper depletion occurring in large (fast growing) individuals causes their energy reserves to be lower at their arrival in the spawning grounds (red line in Figure 2b) than in small (slow growing) individuals (blue line in Figure 2b). As a result, large individuals have lower fecundity than small ones.

The lifetime reproductive output reaches a maximum when an individual experiences both low costs of the breeding migration and high food abundance in the ocean (right-top corner in Figure 3). In contrast, the lifetime reproductive output is at a minimum when it experiences high costs of the breeding migration and high food abundance in the ocean (right-bottom corner in Figure 3). As a consequence, when the migration costs are low, a decline in food abundance in the ocean leads to a decrease in the lifetime reproductive output, as expected. However, when the migration costs are high, a decline in food abundance in the ocean leads to an increase in the lifetime reproductive output. This result also holds when the costs of the breeding migration scale superlinearly with the structural mass (see Figure S3). However, when they scale sublinearly with structural mass, a decline in food abundance in the ocean from high to intermediate levels causes a decrease in lifetime reproductive output but an increase IF this decline is from intermediate to low levels; as a result the minimum lifetime reproductive output occurs at around 0.7 times the amount at ad libitum food (see Figure S3).

Up to this point we have shown that the interaction of two stressors has a nonlinear effect on the individual fitness. Specifically, our analysis based on the individual energetics demonstrates that the cumulative effect of the interacting stressors is not the addition of the independent negative effects. In the following section, we explore the consequences of this nonlinear effect on the viability of an anadromous population.

3.2 | Population effects of costs of the breeding migration and changes in ocean food availability

A decline in food availability in the ocean that results in a reduction in feeding level in this habitat from 0.8 to 0.5 times the amount of ad libitum food can cause both a decrease and an increase in the population biomass. Following the decline in food abundance in the ocean, the population biomass decreases when the costs of the breeding migration are low, whereas it increases when the costs of the breeding migration are high (Figure 4). This unexpected population effect is the consequence of higher energy spent during the breeding migration by larger (better-fed) individuals, and it is robust to sublinear and superlinear scaling factors of the migration costs (see Figure S4).

An analysis of the combined effect of costs of the breeding migration and feeding level in the ocean reveals that, as expected, the highest population biomass occurs when the feeding level in the ocean is high and the costs of the breeding migration are low. High costs of the breeding migration result in extinction when the feeding level in the ocean is high. But surprisingly, a low feeding level in the ocean enables persistence when migration costs are high (Figure 5). Although there are quantitative differences between the individual lifetime reproductive output and the population biomass effects due to density dependence—considered only when investigating the population effects—, they follow a similar qualitative pattern (Figures 3 vs. 5). Hence, the individual nonlinear effects described in the previous section determine to a large extent the effects of the two stressors on the population dynamics.

4 | DISCUSSION

Rapid environmental change has exposed migratory fish to a wide range of stressors, including increased costs of the breeding migration (Caudill et al., 2007; Mesa & Magie, 2006) and reduced food abundance in the ocean (Friedland et al., 2009). We present here an analysis of the life-history and population effects of these stressors and demonstrate that their cumulative effect is not the result of a simple addition of the independent negative effects, but that their interaction is highly nonlinear. We show that low marine food abundances can mitigate the negative effects of high energetic costs of the breeding migration. The mechanism underlying this counterintuitive result arises from the fact that large individuals spend more energy than small ones transporting their body upstream (Bowerman et al., 2017; Glebe & Leggett, 1981; Jonsson et al., 1997) and that a low food level in the ocean influences the individual energetics in two ways: 1) it entails a lower growth potential and therefore a smaller body size and, 2) it causes a small increase in food availability during the habitat switch.

The increase in food availability during the switch from freshwater to seawater leads to an increase in growth rates but a decrease in energy density in wild salmon (MacFarlane, 2010) with individuals after the habitat switch apparently allocating more energy to somatic growth (structural mass) and less to energy storage (reversible mass; Johansen et al., 2001; see Figure S5). Such bias towards increased growth at the expense of energy storage following an increase in food also occurs in various other vertebrate (Auer et al., 2010; Sinervo & Doughty, 1996; Tab orsky, 2006) and invertebrate (Kleinteich et al., 2015; Zeller & Koella, 2016) species. Individuals of these species compensate their growth after an experimental period of food rationing and reach similar sizes as when experiencing continuously high food levels, at the expense of lower fecundity (see Table S1; Figure S6).

Most model formulations for energy allocation of ectotherms in the literature fall into one of two families: the net production and net assimilation models (also known as κ-rule models; Noonburg et al., 1998). Only the latter family of models successfully predicts the increase in somatic growth at the expense of energy density after a transition from low to high food levels observed in diverse taxa (see Appendix S2). The model developed by Martin et al. (2017) for energy allocation of fish, that we use in this study, belongs to this family of models. These models furthermore predict that the bias towards 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 increase in food during the habitat switch do not only grow larger (are bigger), but have a lower energy density (are leaner). Therefore, if food is abundant in the marine habitat, this increases the vulnerability of populations exposed to elevated migration costs because individuals experience a larger step-up change in food levels, resulting in larger sizes but lower energy densities.

The analysis of individual energetic dynamics predicts that high costs of the breeding migration should favour small individuals over large, and conversely, low costs should favour large over small. Therefore, wild populations that naturally differ in their energetic costs of migration, for instance due to distance and elevation differences in the breeding travel, may have diverged in their adaptations to opposing selective pressures. Accordingly, wild populations of sockeye salmon *Oncorhynchus nerka* experiencing naturally high costs of the breeding migration are composed of smaller individuals with more fusiform body shape than populations facing lower costs of the breeding migration (Crossin et al., 2004). Although both body size and body shape are important for adaptation to a costly migration in wild populations, in the face of rapid environmental change it is reasonable to expect that plastic reductions in body size have a higher contribution to adaptation than a less plastic trait such as body shape. In fact, a meta-analysis of wild animal populations suggests that the contribution of phenotypic plasticity to adaptation is greater than that of genetic evolution in response to environmental change (Hendry et al., 2008). Therefore, factors causing a plastic reduction in growth potential, such as a decline in food availability, may have an important contribution to the persistence of these populations.

Motivated by this, we searched for empirical observations to explore the prediction that a decline in food availability and thus in growth potential in the ocean increases the biomass of a population when costs of the breeding migration are high. Since, in wild populations, energetic costs of the breeding migration increase with distance travelled in freshwater (Crossin et al., 2004; Glebe & Leggett, 1981; Jonsson & Jonsson, 2003), we use migration distance as a proxy of energetic costs of the breeding migration in two Atlantic salmon populations. In accordance with our model prediction, the salmon populations from the Imsa (Jonsson & Jonsson, 2016) and the North Esk river (ASFB, 2010) have shown a decrease and an increase in abundance respectively. While in the same period, growth in the ocean has decreased in both populations (Friedland et al., 2009; Jonsson & Jonsson, 2004; Figure 6). Salmon in the Imsa river (river length ~1 km, in Norway) migrate short distances in freshwater while in the North Esk river (river length > 100 km, in Scotland) they migrate long distances and hence face higher energetic costs of the breeding migration. Additional analysis comparing other anadromous populations is needed for more compelling evidence that support our model predictions. Ideally, future analysis should take into account other abiotic factors that affect the migration costs in addition to migration distance, such as elevation travelled, river flow and temperature (Crossin et al., 2004; Martin et al., 2015). However, the comparison of these two wild populations shed light on the potential for contrasting responses to the same stressor in populations experiencing different natural conditions. Remarkably, our model offers a mechanistic explanation for these divergent responses in populations facing a declining trend in marine food availability.

Various consequences for the conservation and fisheries industry of anadromous species arise from the prediction that populations facing high energetic costs of the breeding migration have increased extinction risk when food availability in the ocean, and therefore the growth potential, is high. In particular, increased costs of migration by infrastructure construction in the freshwater habitat are more likely to result in extinction of anadromous populations migrating to a highly productive marine habitat, especially if these negative impacts occur in a time frame that is too short for an evolutionary response towards, for example, slow body growth rate and other physiological and morphological adaptations for an energetically costly upriver travel (Eliason et al., 2011). Although the rate at which dams were completed declined from around 1,000 a year in the 1970s to around 260 a year in the 1990s, during the first decades of the 20th century the number of large dams increased with on average more than 500 new dams annually from 45,000 (WCD, 2000) to 55,000 (ICOLD, 2017). This trend implies that an increasing number of anadromous populations are facing higher costs of the breeding migration, possibly resulting in local extinction or selection for smaller body sizes with negative effects for fisheries in either case. Paradoxically, the decline of food levels in the Northeast Atlantic during the last decades may have mitigated the collapse of Atlantic salmon populations due to increased infrastructure building in freshwater streams. In the upcoming decades marine productivity is predicted to continue dropping due to climate change (Hoegh-Guldberg

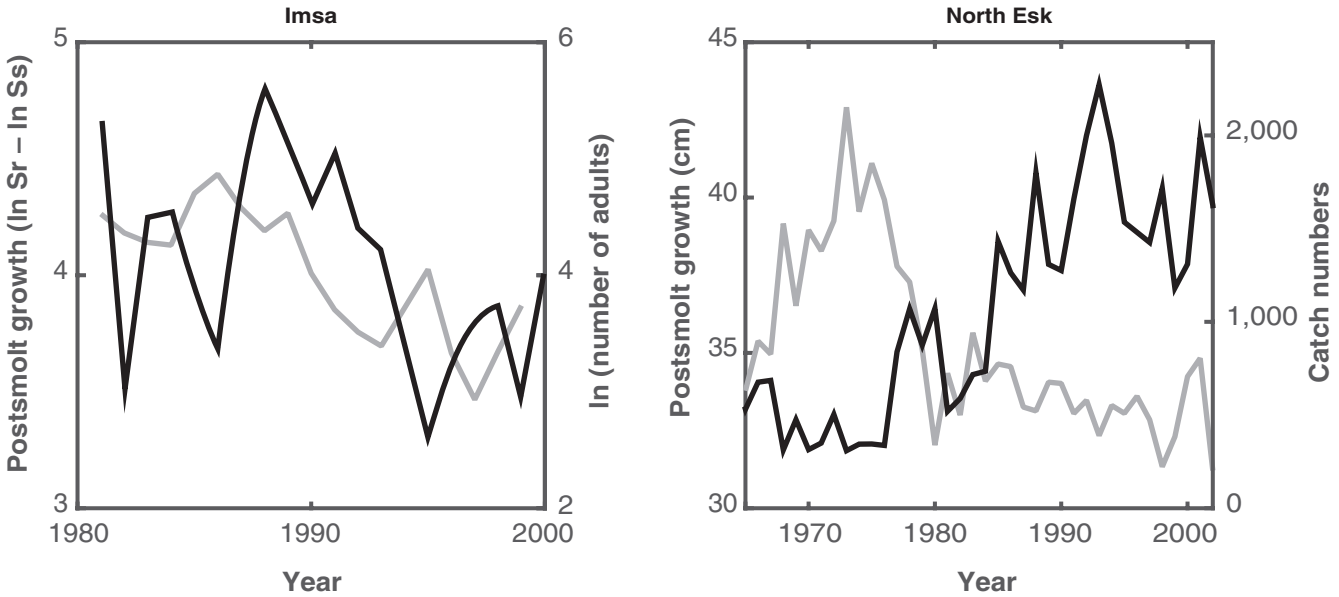

FIGURE 6 Postsmolt growth increment (grey) as either ln Sr - ln Ss in Imsa (where Sr is the mass of returning adults and Ss is the mass of the same fish as smolts, Jonsson & Jonsson, 2004) or back-calculated growth increment in North Esk (Friedland et al., 2009). And population abundance (black) as either log of adult number (Imsa; Jonsson & Jonsson, 2016) or catch numbers (North Esk; ASFB, 2010)

& Bruno, 2010; Moore et al., 2018), with a potential negative effect in food levels for Atlantic salmon, which although bad for fisheries, may benefit anadromous population persistence.

Other factors may affect the persistence of anadromous populations facing concurrently high costs of the breeding migration and declining food availability in ocean. After the habitat switch, size-dependent predation mortality risk increases and therefore high food availability in the ocean that enables high body growth rate increases survival in the first marine stage (Friedland et al., 2009) favouring the persistence of threatened populations. Reduced size-dependent predation mortality risk could be the result either of a high growth rate during the first marine stage or of reaching a large body size before the habitat switch. In fact, a long-term study of Atlantic salmon in the Simojoki river shows that survival during the marine phase is positively correlated with body size at the habitat switch (Jutila et al., 2006). Moreover, the body size at the habitat switch in this population is negatively correlated with the individual density in the freshwater habitat (Jutila et al., 2006); therefore large body sizes at the habitat switch are reached when population abundance is low in this habitat. This is the consequence of relaxed density dependence enabling a high body growth rate (Chaparro-Pedraza & de Roos, 2019; Walters et al., 2013). Since threatened anadromous populations have relatively low population abundance, this suggests that its individuals are more likely to reach a larger body size at the habitat switch and therefore to experience lower predation mortality once in the ocean. Further research is necessary to understand how size-dependent predation mortality interacts with reduced food availability in the ocean and high costs of the breeding migration accounting for density-dependence effects in the freshwater habitat.

Current environmental changes increase the variety and intensity of stressors affecting ecological communities in cumulative and interactive ways (Crain et al., 2008), making the need to understand the mechanisms generating interactive effects an urgent matter (Orr et al., 2020). We have demonstrated how such mechanisms can be investigated linking individual energy budgets and individual life history, and have shown that two stressors with independent negative effects interact in a highly nonlinear manner and mitigate each other. Given that environmental change comes with other stressors such as warming trends in the spawning streams that also affect individual energetics and thus life history (Eliason et al., 2011; Jonsson & Jonsson, 2009) and that are currently co-occurring with the stressors investigated in this study, the consequences of these multiple interacting stressors on anadromous populations need further research. For this purpose, as we show in the present study, the description of the life history based on individual energetics is essential for a mechanistic understanding of their effects at the population and community levels. Our results show that in the face of multiple environmental threats the outcome of conservation efforts aimed at population persistence (e.g. increasing growth rate during oceanic life stage of Atlantic salmon) may in fact promote extinction and highlight the need for accurately predicting ecological consequences of environmental change. If we are to predict ecological consequences of environmental change a mechanistic understanding linking individual energy budgets, life history and population dynamics will be almost certainly required.

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AUTHORS' CONTRIBUTIONS

P.C.C.-P. and A.M.d.R. designed methodology; P.C.C.-P. analysed the results and led the writing of the chapter; A.M.d.R. contributed to later versions of the manuscript.

DATA AVAILABILITY STATEMENT

No new data were collected and used for this study.

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REFERENCES

Alexander, R. (1998). When is migration worthwhile for animals that walk, swim or fly? *Journal of Avian Biology*, *29*(4), 387–394.

ASFB. (2010). *Annual review*. Association of Salmon Fishery Boards. http://fms.scot/wp-content/uploads/2017/02/ASFB-Review-2010.pdf

Auer, S. K., Arendt, J. D., Chandramouli, R., & Reznick, D. N. (2010). Juvenile compensatory growth has negative consequences for reproduction in Trinidadian guppies (*Poecilia reticulata*). *Ecology Letters*, *13*(8), 998–1007. https://doi.org/10.1111/j.1461-0248.2010.01491.x

Bjornn, T. C., Reischel, T. S., Ringe, R. R., Tolotti, K. R., & Stuehrenberg, L. S. (1999). *Radio telemetry assessments of migration patterns and fallbacks of adult salmon and steelhead in the forebay of Bonneville Dam, 1997–1998*. U.S. Army Corps of Engineers. https://www.lib.uidaho.edu/digital/ferl/data/ferl-tr-99-1.html

Bley, P. W., & Moring, J. R. (1988). *Freshwater and ocean survival of Atlantic salmon and steelhead: A synopsis* (Vol. *88*). U.S. Fish and Wildlife Service.

Bowerman, T. E., Pinson-Dumm, A., Peery, C. A., & Caudill, C. C. (2017). Reproductive energy expenditure and changes in body morphology for a population of Chinook salmon *Oncorhynchus tshawytscha* with a long distance migration. *Journal of Fish Biology*, *1–20*, https://doi.org/10.1111/jfb.13274

Caudill, C. C., Daigle, W. R., Keefer, M. L., Boggs, C. T., Jepson, M. A., Burke, B. J., Zabel, R. W., Bjornn, T. C., & Peery, C. A. (2007). Slow dam passage in adult columbia river salmonids associated with unsuccessful migration: Delayed negative effects of passage obstacles or condition-dependent mortality? *Canadian Journal of Fisheries and Aquatic Science*, *64*, 979–995. https://doi.org/10.1139/F07-065

Chaparro-Pedraza, P. C., & de Roos, A. M. (2019). Environmental change effects on life-history traits and population dynamics of anadromous fishes. *Journal of Animal Ecology*, *88*(8), 1178–1190. https://doi.org/10.1111/1365-2656.13010

Crain, C. M., Kroeker, K., & Halpern, B. S. (2008). Interactive and cumulative effects of multiple human stressors in marine systems. *Ecology Letters*, *11*(12), 1304–1315. https://doi.org/10.1111/j.1461-0248.2008.01253.x

Crossin, G. T., Hinch, S. G., Farrell, A. P., Higgs, D. A., Lotto, A. G., Oakes, J. D., & Healey, M. C. (2004). Energetics and morphology of sockeye salmon: Effects of upriver migratory distance and elevation. *Journal of Fish Biology*, *65*(3), 788–810. https://doi.org/10.1111/j.1095-8649.2004.00486.x

Dauble, D. D., & Mueller, R. P. (2000). Upstream passage monitoring: Difficulties in estimating survival for adult chinook salmon in the Columbia and snake rivers. *Fisheries*, *25*(8), 24–34. https://doi.org/10.1577/1548-8446(2000)025<0024:upmdie>2.0.co;2

de Roos, A. M. (1988). Numerical methods for structured population models: The escalator boxcar train. *Numerical Methods for Partial Differential Equations*, *4*(3), 173–195. https://doi.org/10.1002/num.1690040303

Doucett, R. R., Booth, R. K., Power, G., & McKinley, R. S. (1999). Effects of the spawning migration on the nutritional status of anadromous Atlantic salmon (*Salmo salar*): Insights from stable-isotope analysis. *Canadian Journal of Fisheries and Aquatic Sciences*, *56*(11), 2172–2180. https://doi.org/10.1139/cjfas-56-11-2172

Eliason, E. J., Clark, T. D., Hague, M. J., Hanson, L. M., Gallagher, Z. S., Jeffries, K. M., Gale, M. K., Patterson, D. A., Hinch, S. G., & Farrell, A. P. (2011). Differences in thermal tolerance among sockeye salmon populations. *Science*, *332*(6025), 109–112. https://doi.org/10.1126/science.1199158

FAO. (2016). The state of world fisheries and aquaculture 2016. Contributing to food security and nutrition for all. Rome. 200 pp.

Friedland, K. D., MacLean, J. C., Hansen, L. P., Peyronnet, A. J., Karlsson, L., Reddin, D. G., Maoiléidigh, N. Ó., & McCarthy, J. L. (2009). The recruitment of Atlantic salmon in Europe. *ICES Journal of Marine Science*, *66*(2), 289–304. https://doi.org/10.1093/icesjms/fsn210

Glebe, B. D., & Leggett, W. C. (1981). Latitudinal differences in energy allocation and use during the freshwater migrations of American shad (*Alosa sapidissima*) and their life history consequences. *Canadian Journal of Fisheries and Aquatic Sciences*, *38*(7), 806–820. https://doi.org/10.1139/f81-109

Hendry, A. P., Farrugia, T. J., & Kinnison, M. T. (2008). Human influences on rates of phenotypic change in wild animal populations. *Molecular Ecology*, *17*(1), 20–29. https://doi.org/10.1111/j.1365-294X.2007.03428.x

Hendry, K., & Cragg-Hine, D. (2003). *Ecology of the Atlantic salmon. Conserving natura 2000 rivers ecology series no. 7*. English Nature.

Hinch, S. G., & Rand, P. S. (2000). Optimal swimming speeds and forward-assisted propulsion: Energy-conserving behaviours of upriver-migrating adult salmon. *Canadian Journal of Fisheries and Aquatic Science*, *57*, 2470–2478. https://doi.org/10.1139/f00-238

Hoegh-Guldberg, O., & Bruno, J. F. (2010). The impact of climate change on the world's marine ecosystem. *Science*, *328*, 1523–1528. https://doi.org/10.1080/00330124.2015.1124788

Hughes, N. F. (2004). The wave-drag hypothesis: An explanation for size-based lateral segregation during the upstream migration of salmonids. *Canadian Journal of Fisheries and Aquatic Sciences*, *61*(1), 103–109. https://doi.org/10.1139/f03-144

Hutchings, J. A., & Jones, M. E. B. (1998). Life history variation and growth rate thresholds for maturity in Atlantic salmon, *Salmo salar*. *Canadian Journal of Fisheries and Aquatic Sciences*, *55*, 22–47. https://doi.org/10.1139/cjfas-55-S1-22

ICOLD. (2017). World register of dams. https://www.icold-cigb.org

Jager, T., Martin, B. T., & Zimmer, E. I. (2013). DEBkiss or the quest for the simplest generic model of animal life history. *Journal of Theoretical Biology*, *328*, 9–18. https://doi.org/10.1016/j.jtbi.2013.03.011

Johansen, S. J. S., Ekli, M., Stangnes, B., & Jobling, M. (2001). Weight gain and lipid deposition in Atlantic salmon, *Salmo salar*, during compensatory growth: Evidence for lipostatic regulation? *Aquaculture Research*, *32*(12), 963–974. https://doi.org/10.1046/j.1365-2109.2001.00632.x

Jonsson, B., & Jonsson, N. (2004). Factors affecting marine production of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, *61*(12), 2369–2383. https://doi.org/10.1139/f04-215

Jonsson, B., & Jonsson, N. (2009). A review of the likely effects of climate change on anadromous Atlantic salmon *Salmo salar* and brown trout *Salmo trutta*, with particular reference to water temperature and flow. *Journal of Fish Biology*, *75*(10), 2381–2447. https://doi.org/10.1111/j.1095-8649.2009.02380.x

Jonsson, B., & Jonsson, N. (2016). Fecundity and water flow influence the dynamics of Atlantic salmon. *Ecology of Freshwater Fish*, *26*(3), 497–502. https://doi.org/10.1111/eff.12294

Jonsson, N., & Jonsson, B. (2003). Energy allocation among developmental stages, age groups, and types of Atlantic salmon (*Salmo salar*) spawners. *Canadian Journal of Fisheries and Aquatic Sciences*, *60*(5), 506–516. https://doi.org/10.1139/F03-042

Jonsson, N., Jonsson, B., & Hansen, L. P. (1997). Changes in proximate composition and estimates of energetic costs during upstream migration and spawning in Atlantic salmon *Salmo salar*. *Journal of Animal Ecology*, *66*(3), 425–436. https://doi.org/10.2307/5987

Jonsson, N., Jonsson, B., & Hansen, L. P. (1998). The relative role of density-dependent and density-independent survival in the life cycle of Atlantic salmon *Salmo salar*. *Journal of Animal Ecology*, *67*(5), 751–762. https://doi.org/10.1046/j.1365-2656.1998.00237.x

Jutila, E., Jokikokko, E., & Julkunen, M. (2006). Long-term changes in the smolt size and age of Atlantic salmon, *Salmo salar* L., in a Northern Baltic River related to parr density, growth opportunity and post-smolt survival. *Ecology of Freshwater Fish*, *15*(3), 321–330. https://doi.org/10.1111/j.1600-0633.2006.00171.x

Kleinteich, A., Wilder, S. M., & Schneider, J. M. (2015). Contributions of juvenile and adult diet to the lifetime reproductive success and lifespan of a spider. *Oikos*, *124*(2), 130–138. https://doi.org/10.1111/oik.01421

Kooijman, S. A. L. M. (2010). *Dynamic energy budget theory for metabolic organisation* (Vol. 1). https://doi.org/10.1098/rstb.2010.0167

Kooijman, S. A. L. M., & Metz, J. A. J. (1984). On the dynamics of chemically stressed populations: The deduction of population consequences from effects on individuals. *Hydrobiological Bulletin*, *17*(1), 88–89. https://doi.org/10.1007/BF02255198

Koskela, J., Pirhonen, J., & Jobling, M. (1997). Feed intake, growth rate and body composition of juvenile Baltic salmon exposed to different constant temperatures. *Aquaculture International*, *5*, 351–360.

Leggett, W. C., & Power, G. (1969). Differences between two populations of landlocked Atlantic salmon (*Salmo salar*) in Newfoundland. *Journal of the Fisheries Research Board of Canada*, *26*(6), 1585–1596. https://doi.org/10.1139/f69-142

Lenders, H. J. R., Chamuleau, T. P. M., Hendriks, A. J., Lauwerier, R. C. G. M., Leuven, R. S. E. W., & Verberk, W. C. E. P. (2016). Historical rise of waterpower initiated the collapse of salmon stocks. *Scientific Reports*, *6*, 1–9. https://doi.org/10.1038/srep29269

Limburg, K. E., & Waldman, J. R. (2009). Dramatic declines in north Atlantic diadromous fishes. *BioScience*, *59*(11), 955–965. https://doi.org/10.1525/bio.2009.59.11.7

MacFarlane, R. B. (2010). Energy dynamics and growth of Chinook salmon (*Oncorhynchus tshawytscha*) from the central valley of California during the Estuarine phase and first ocean year. *Canadian Journal of Fisheries and Aquatic Sciences*, *67*(10), 1549–1565. https://doi.org/10.1139/F10-080

Martin, B. T., Heintz, R., Danner, E. M., & Nisbet, R. M. (2017). Integrating lipid storage into general representations of fish energetics. *Journal of Animal Ecology*, *86*(4), 812–825. https://doi.org/10.1111/1365-2656.12667

Martin, B. T., Nisbet, R. M., Pike, A., Michel, C. J., & Danner, E. M. (2015). Sport science for salmon and other species: Ecological consequences of metabolic power constraints. *Ecology Letters*, *18*(6), 535–544. https://doi.org/10.1111/ele.12433

Mccormick, S. D., Hansen, L. P., Quinn, T. P., & Saunders, R. L. (1998). Movement, migration, and smolting of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, *55*, 77–92. https://doi.org/10.1139/d98-011

Mesa, M., & Magie, C. (2006). Evaluation of energy expenditure in adult spring Chinook salmon migrating upstream in the Columbia River Basin: An assessment based on sequential proximate analysis. *River Research and Applications*, *22*, 1085–1095. https://doi.org/10.1002/rra

Moore, J. K., Fu, W., Primeau, F., Britten, G. L., Lindsay, K., Long, M., Doney, S. C., Mahowald, N., Hoffman, F., & Randerson, J. T. (2018). Sustained climate warming drives declining marine biological productivity. *Science*, *359*(6380), 1139–1143. https://doi.org/10.1126/science.aao6379

Nisbet, R. M., Muller, E. B., Lika, K., & Kooijman, S. A. L. M. (2000). From molecules to ecosystems through dynamic energy budget models. *Journal of Animal Ecology*, *69*(6), 913–926. https://doi.org/10.1046/j.1365-2656.2000.00448.x

Noonburg, E. G., Nisbet, R. M., McCauley, E., Gurney, W. S. C., Murdoch, W. W., & De Roos, A. M. (1998). Experimental testing of dynamic energy budget models. *Functional Ecology*, *12*(2), 211–222. https://doi.org/10.1046/j.1365-2435.1998.00174.x

Orr, J. A., Vinebrooke, R. D., Jackson, M. C., Kroeker, K. J., Kordas, R. L., Mantyka-Pringle, C., van den Brink, P. J., De Laender, F., Stoks, R., Holmstrup, M., Matthaei, C. D., Monk, W. A., Penk, M. R., Leuzinger, S., Schäfer, R. B., & Piggott, J. J. (2020). Towards a unified study of multiple stressors: Divisions and common goals across research disciplines. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1926). https://doi.org/10.1098/rspb.2020.0421

Pecquerie, L., Johnson, L. R., Kooijman, S. A. L. M., & Nisbet, R. M. (2011). Analyzing variations in life-history traits of Pacific salmon in the context of dynamic energy budget (DEB) theory. *Journal of Sea Research*, *66*(4), 424–433. https://doi.org/10.1016/j.seares.2011.07.005

Persson, L., Leonardsson, K., De Roos, A. M., Gyllenberg, M., & Christensen, B. (1998). Ontogenetic scaling of foraging rates and the dynamics of a size-structured consumer-resource model. *Theoretical Population Biology*, *54*(3), 270–293. https://doi.org/10.1006/tpbi.1998.1380

Potts, W. T. W., & Rudy, P. P. (1969). Water balance in the eggs of the Atlantic salmon *Salmo salar*. *The Journal of Experimental Biology*, *50*, 223–237.

Shearer, K., Asgard, T., Andorsdottir, G., & Aas, G. (1994). Whole body elemental and proximate composition of Atlantic salmon (*Salmo salar*) during the life cycle. *Journal of Fish Biology*, *44*, 785–797. https://doi.org/10.1111/j.1095-8649.1994.tb01255.x

Sinervo, B., & Doughty, P. (1996). Interactive effects of offspring size and timing of reproduction on offspring reproduction: Experimental, maternal, and quantitative genetic aspects. *Evolution*, *50*(3), 1314–1327.

Taborsky, B. (2006). The influence of juvenile and adult environments on life-history trajectories. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1587), 741–750. https://doi.org/10.1098/rspb.2005.3347

Thorpe, J. E., Mangel, M., Metcalfe, N. B., & Huntingford, F. A. (1998). Modelling the proximate basis of salmonid life-history variation, with application to Atlantic salmon, *Salmo salar* L. *Evolutionary Ecology*, *12*(5), 581–599. https://doi.org/10.1023/A:1022351814644

Thorpe, J. E., Miles, M. S., & Keay, D. S. (1984). Developmental rate, fecundity and egg size in Atlantic salmon, *Salmo Salar* L. *Aquaculture*, *43*, 289–305. https://doi.org/10.1016/0044-8486(84)90030-9

Walters, A. W., Copeland, T., & Venditti, D. A. (2013). The density dilemma: Limitations on juvenile production in threatened salmon populations. *Ecology of Freshwater Fish*, *22*(4), 508–519. https://doi.org/10.1111/eff.12046

WCD. (2000). *Dams and development: A new framework for decision-making*. Earthscan Publications. https://doi.org/10.1097/GCO.0b013e3283432017

West, G. B., Brown, J. H., & Enquist, B. J. (2001). A general model for ontogenetic growth. *Nature*, *413*(6856), 628–631. https://doi.org/10.1038/35098076

Zeller, M., & Koella, J. C. (2016). Effects of food variability on growth and reproduction of aedes aegypti. *Ecology and Evolution*, *6*(2), 552–559. https://doi.org/10.1002/ece3.1888

SUPPORTING INFORMATION

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

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