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### Authors

Yang, Luojun  
Waples, Robin S  
Baskett, Marissa L

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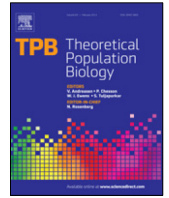
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# Life history and temporal variability of escape events interactively determine the fitness consequences of aquaculture escapees on wild populations

Luojun Yang<sup>a,b,\*</sup>, Robin S. Waples<sup>c</sup>, Marissa L. Baskett<sup>a</sup>

<sup>a</sup> Department of Environmental Science and Policy, University of California, Davis, One Shields Avenue, Davis, CA 95616-5270, USA

<sup>b</sup> School of Life Sciences, Nanjing University, 163 Xianlin Road, Qixia District, Nanjing, Jiangsu Province, 210023, PR China

<sup>c</sup> Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 2725 Montlake Boulevard East, Seattle, WA 98112-2097, USA

## HIGHLIGHTS

- Constant low-level escapees can have greater fitness effects than large spikes.
- The relative effects of constant vs. variable spillover are robust to age structure.
- Species with longer generation time experience greater fitness effects of escapees.
- Early maturity in captivity causes greater fitness effects on shorter-lived species.

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## ABSTRACT

Domesticated individuals are likely to be maladaptive in the wild due to adaptation to captivity. Escaped aquaculture fish can cause unintended fitness and demographic consequences for their wild conspecifics through interbreeding and competition. Escape events from different sources exhibit great heterogeneity in their frequencies and magnitudes, ranging from rare but large spillover during a storm, to continuous low-level leakage caused by operational errors. The timescale of escape events determines the distribution of gene flow from aquaculture to the wild. The evolutionary consequences of this variation in timescale will depend on the degree of generation overlap and the focal species' life history attributes, especially those under selection in aquaculture (e.g., growth rate, which can influence additional demographically important traits such as age at maturity). To evaluate the effects of variable escape both within and across generations, we construct an age-structured model of coupled genetic and demographic dynamics and parameterize it for species with contrasting life history characteristics (*Salmo salar* and *Gadus morhua*). Our results are consistent with earlier discrete-generation models that constant, low-level spillover can have a greater impact than rare, large pulses of leakage, even after accounting for the averaging effects of overlapping generations. The age-structured model also allows detailed evaluation of the role of different life history traits, which reveals that species with longer generation times might experience greater fitness consequences of aquaculture spillover but are less sensitive to variability in spillover. Additionally, environment-induced earlier maturity of escapees can increase the fitness effects on wild fish, especially those with shorter generation times. Our results suggest that effective management to minimize the unintended fitness consequences of aquaculture releases might require extensive monitoring efforts on constant, low-level spillover and assessment of the focal species' life history characteristics.

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## 1. Introduction

The gene flow resulting from intentional or unintentional release of domesticated organisms to the wild has potential detrimental effects on the persistence of wild populations (Rhymer and Simberloff, 1996; Laikre et al., 2010). Due to adaptation to captivity, domesticated escapees are likely to have lower fitness

\* Correspondence to: Department of Ecology and Evolutionary Biology, 106A Guyot Hall, Princeton University, Princeton, NJ 08544-2016, USA.  
E-mail address: [luojuny@princeton.edu](mailto:luojuny@princeton.edu) (L. Yang).

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in the wild compared to native individuals (Frankham, 2008). Thus, by interbreeding and interacting with wild conspecifics, escapees can increase wild populations' risk of extinction through fixation of deleterious traits (Lynch and O'Hely, 2001), intensified competition for resources (Jonsson and Jonsson, 2006), and disease spread (Naylor et al., 2005).

Escape of aquacultured fish to the wild is a prototypical example of strong, stochastic gene flow from domesticated to natural populations. In this study, we focus on unintentional releases from commodity aquaculture, which involves raising fish in contained facilities primarily for food production, in contrast to hatcheries for restorative release or fisheries enhancement. Aquaculture is a rapidly growing industry: with the share of world aquaculture production in total fish consumption having increased from 7% in 1974 to 44.1% in 2014 (FAO, 2016), aquaculture fish often outnumber their local wild counterparts (Naylor et al., 2005; Hansen and Windsor, 2006). For marine finfish, the typical approach of raising them is in net pens in the ocean. As a result of net damages from storm events, biting behavior, or operational errors (Jackson et al., 2015), large number of cultured fish escape into the wild every year. For example, 1.18 million (236,400 yr<sup>-1</sup>) Atlantic salmon (*Salmo salar*), one of the most commonly commercially cultured marine fish, escaped from Norwegian farms during 2010–2014 (Norwegian Directorate of Fisheries, 2017), while the estimated number of wild spawners is only 530,000 in 2017 (Norwegian Institute for Nature Research (NINA), 2018). The reported number of escaped Atlantic cod (*Gadus morhua*) has been much lower due to lower production (0.30 million escaped during 2010–2014, or 59,800 yr<sup>-1</sup>, reported by Norwegian Directorate of Fisheries, 2017). However, cod tend to bite the net cage and actively search for holes in the net cage wall (Moe et al., 2007), resulting in a higher rate of escaping (1.02% cod versus 0.19% salmon escaped from aquaculture during 2001–2009 in Norway, according to Jensen et al., 2010).

Empirical observations suggest that escaped Atlantic salmon can spawn in the wild (Glover et al., 2017), and genetic analyses further indicate substantial level of introgression between cultured and wild individuals in Norwegian rivers (Karlsson et al., 2016; Glover et al., 2017). The genetic difference between cultured and locally adapted wild fish then can result in hybrids with intermediate traits (Glover et al., 2009; Fraser et al., 2010) as well as reduced lifetime success in natural environment (Hindar et al., 1991; McGinnity et al., 2003). Theoretical models also predict that aquaculture escapees can have long-term genetic effects on wild populations (Tufto, 2001, 2017), and may pose a threat of extinction when the wild population size is small (Weir and Grant, 2005; Ford and Myers, 2008). Although little is known about the ecological and genetic effects of escaped aquaculture fish of species beyond salmon, such as Atlantic cod, the negative consequences are likely to be substantial (Bekkevold et al., 2006; Uglem et al., 2008).

Reports of detection of escaped aquaculture fish cover a wide geographical range and vary substantially in time. For example, the mean proportion of aquaculture-origin Atlantic salmon in eastern North American rivers ranges from 0.2% to 36.3% during 1990–2006, with the overall fluctuations from 0% to 100% (Morris et al., 2008). One source of this variability is rare, large escape events, which, while a small fraction of the total escape events, account for the majority of reported numbers for aquaculture spillover (Jackson et al., 2015). Therefore, researchers argue that focusing on preventing these massive incidences would be the most efficient way to minimize the fitness effects of aquaculture spillover (Jensen et al., 2010). However, the reported number of escapees are likely to be underestimated, partly due to many cases of undetected, or unreported, small-scale escape events. Meta-analysis suggests that the actual number of escaped aquaculture salmon can be 2–4 fold as high as the reported number in

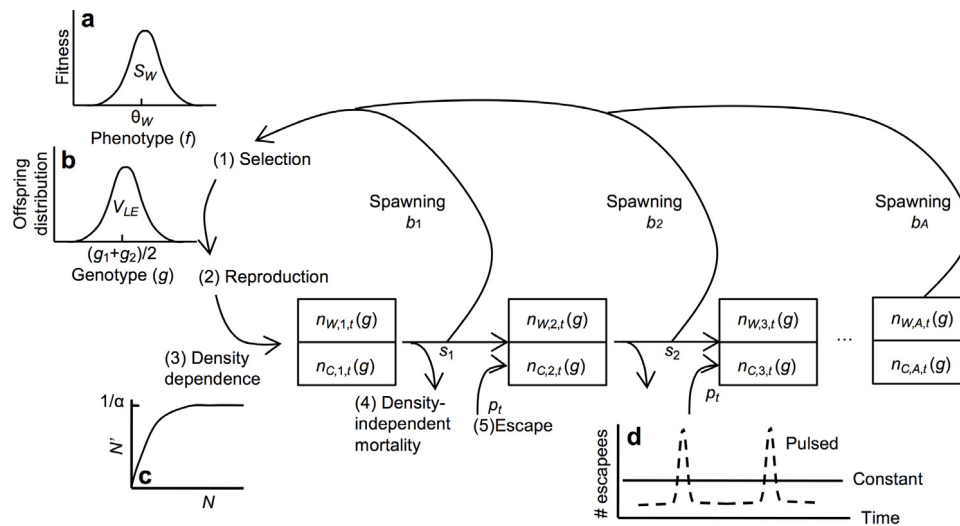
Norway (Skilbrei et al., 2014). Even though improvement in net pen security can help prevent the large escape events and drastically reduce the reported number of escapees (as is the case in British Columbia, Canada; DFO, 2017), the largely undocumented “trickle” losses of fish from the net pens might still contribute to the unintended fitness consequences on wild populations. This might be particularly important in the aquaculture management of Atlantic cod, for which the “trickle” losses through holes in the net cage are more likely (Moe et al., 2007).

In our previous modeling results, when assuming equal number of average escapees over time, constant small-scale leakage can have a greater fitness effect on wild populations compared with pulsed, large escape events (Baskett et al., 2013). Intuitively, this is because strong selection can reverse maladaptive effects during the intervals between large escape events. Although the constant leakage of aquaculture escapees into the wild has lesser short-term effects, as found in Hindar et al. (2006), these effects accumulate to a greater total outcome over time due to the continuous fitness pressure imposed (analogous to a “migrational meltdown”, Ronce and Kirkpatrick, 2001). This finding is also consistent with the broader emerging theory indicating that stochastic dispersal can increase the potential for local adaptation in connected populations experiencing differential selection (Fife and Peletier, 1981; Lenormand and Raymond, 2000; Rice and Papadopoulos, 2009; Rice et al., 2011).

Determining the generality and robustness of this potential for greater fitness consequences from trickle losses of aquaculture fish compared to pulsed, large escape events requires consideration of age structure with overlapping generations for different life histories. Modeling overlapping generations with explicit age structure might alter the expectations for the effect of variable spillover compared to assuming discrete-non-overlapping generations, as done for simplicity in Baskett et al. (2013), for two reasons. First, because many aquacultured fish species are iteroparous, repeated reproduction of aquaculture escapees in the wild might average the effect of a pulsed, large spillover over time, thus narrowing the difference between pulsed and constant spillover. Second, most species targeted for marine aquaculture are relatively long-lived and the lifespan of some species (e.g., Atlantic cod) can be longer than twenty years (Table 2 in Waples et al., 2012), which is much greater than the approximate cycle of temporal variability in spillover (Morris et al., 2008; Jensen et al., 2010). Therefore, a generational timescale cannot appropriately capture the timescale and dynamical consequences of variable spillover. Slower life histories with longer lifespans and lower annual per-capita fecundity (as is the case for Atlantic cod) might lead to more averaging in time, but the wild population might also experience a greater proportional effect of aquaculture release and its variation. Disentangling these generational and vital rate effects is necessary to understand how life history mediates unintended fitness consequences from aquaculture spillover and its variability in time.

Furthermore, an aquaculture environment optimized for fish growth could lead to accelerated life cycles with earlier ages at maturity (Thorpe, 1991, 2004). When they escape to the wild, these early maturing individuals might yield higher lifetime reproductive output and pose a greater threat to the wild population by both increasing the frequency of maladaptive alleles and reducing the survival rate of wild offspring during intensified early-stage competition. The consequences of such phenotypic changes in life history are likely to be nonlinear and also require consideration of age structure and overlapping generations.

Here we extend the unstructured, discrete-generation model in Baskett et al. (2013) to assess the effect of age structure with overlapping generations and different life histories on the fitness consequences of aquaculture escapees on wild populations. The



**Fig. 1.** Illustration of the age-structured model (Eqs. (2)–(6)). Each year, five life cycle events take place in the order of (1) fecundity selection, (2) reproduction, (3) density-dependent survival, (4) density-independent survival, and (5) escape events. Boxes represent age classes of wild and captive origins (indicated by subscripts) and small graphs describe dynamics at each step: a. stabilizing selection with fitness normally distributed around the optimal trait  $\theta_W$ ; b. inheritance with normal distribution offspring genotype around the parental mean due to random environmental effects; c. Beverton–Holt curve of density-dependent survival, d. sample time series of pulsed (dashed line) and constant (solid line) escape events. See Table 1 for definitions of the parameters indicated.

model tracks coupled demographic and genetic dynamics of the wild population, with inputs from an aquaculture population of constant size and genetic composition. To compare the effect of age structure under different life histories, we parameterize the model with life table data of Atlantic Salmon (*Salmo salar*), which is relatively short-lived with high annual but low life-time reproductive output (Ryman, 1997), and Atlantic Cod (*Gadus morhua*), which has a relatively longer life-span in the wild and lower annual but higher lifetime fecundity (Waples et al., 2013; Kuparinen et al., 2016). We then broaden our investigation into the effect of life history with an exploration of how a range of lifetime fecundity and generation time values affect the fitness consequences of aquaculture escapees on wild populations. Finally, we analyze the effect of environment-driven earlier maturity by altering escapees’ reproductive schedules in our simulations.

**2. Material and methods**

**2.1. Study system**

For our model systems, we choose two example species with contrasting life histories: Atlantic salmon (*Salmo salar*) and Atlantic cod (*Gadus morhua*). Atlantic salmon have a lifespan of 4 to 6 years, whereas Atlantic cod can live more than 20 years in the wild (Froese and Pauly, 2018). Both species are iteroparous. As noted in Section 1 both species are commercially important aquaculture species raised in marine net pens in the same habitat as their wild conspecifics, with significant spillover to wild populations. Usually, aquaculture facilities keep fish in hatcheries during the first year before placement in oceanic net pens and harvest them around the age of maturation. In practice, smolts of Atlantic salmon are placed into the ocean net pens after 15 months in hatcheries, then harvested after 12–18 months rearing in the sea cages.<sup>1</sup> Similarly, cultured Atlantic cod are harvested 24–36 months after hatching (FAO, 2004).

**Table 1**

Model parameters.		
Parameter	Description	Default value
$A$	Maximum age	Species-dependent (see Supplementary Material Appendix C)
$s_x$	Age-dependent survival probability (density-independent)	Species-dependent (see SM Appendix C)
$b_{t,x}$	Age-dependent per-capita maximum reproductive output	Species-dependent (see SM Appendix C)
$r_W$	Relative reproductive success of wild spawners	1
$r_C$	Relative reproductive success of cultured spawners compared to wild spawners	0.8
$\alpha$	Density-dependent parameter for Beverton–Holt function (inverse of the maximum population size)	0.00025
$E$	Environmental variance	0.04
$S$	Width of natural selection function (inversely related to selection strength)	0.1
$\theta_W$	Optimal trait the wild	1
$V_{LE}$	Genetic variance at linkage equilibrium	0.01
$\theta_C$	Mean trait in the aquaculture environment	0–1
$V_C$	Genetic variance in the aquaculture population	0.009
$p_c$	Long-term average of the proportion of escapees over time	0.05

**2.2. Model overview**

We use a quantitative genetic model of a generic trait to model the genetic dynamics, given that many traits under artificial selection are quantitative traits (Hutchings and Fraser, 2008). In contrast to the breeder’s equation, our model follows the full breeding value distribution to account for changes in genetic variance with mixing between populations that experience different selection.

To model overlapping generations, we implement age structure for both wild and aquaculture populations. During a single timestep of a year, five events take place in the order shown in Fig. 1: (1) fecundity selection; (2) reproduction; (3) density-dependent survival, which is common at early life stages for

<sup>1</sup> Personal communication with Kevin Glover, November 2016.

marine fish (Myers, 2001); (4) density-independent survival so that only a fraction of fish in each age class can successfully move on to the next age class; and (5) escape events where post-reproductive age classes receive input from a constant artificially-maintained population with a genetic composition that reflects domestication selection for traits that deviate from the wild optimum. This spillover can occur as low-level, constant leakage every year representing minor net damages, or as sporadic, large pulses of escape, representing storm events. In all cases, we assume the same long-term average number of escapees. The escapees can interbreed with wild individuals, but have lower relative reproductive output due to both non-genetic and genetic effects of domestication.

### 2.3. Mathematical details

Our model follows the age-dependent population density distribution  $n_{i,x,t}(g)$  over genotypes  $g$  of age  $x$  individuals at year  $t$  that originated from population  $i$  ( $W$  for wild and  $C$  for captive). The total number of individuals in each class is  $N_{i,x,t} = \int n_{i,x,t}(g)dg$  and the genotype probability distribution is  $\phi_{i,x,t}(g) = n_{i,x,t}(g)/N_{i,x,t}$ .

*Selection, reproduction, and density dependence.* We first convert genotypes to phenotypes to account for imperfect heritability and then have selection act on phenotypes. Assuming random environmental effects, the phenotype  $f$  of an individual is randomly distributed around its genotype  $g$  with environmental variance  $E$  such that

$$P(f|g) = \frac{1}{\sqrt{2\pi E}} \exp\left(-\frac{(f-g)^2}{2E}\right). \quad (1)$$

Each year, fecundity selection acts on the phenotypes of spawners, where we implement stabilizing selection for optimal trait  $\theta_W$  in the wild with selection strength  $1/S$ . Spawners have a per-capita age-dependent maximum reproductive output of  $b_{i,x}$  (which = 0 before maturity), and deviations from the optimal trait lead to reductions in the reproductive output from the maximum. The population origin  $i$  (wild or captive) will alter this age-specific maximum value if, for example, rearing in the aquaculture environment leads to earlier maturity. Non-genetic effects of rearing in captivity also apply through a factor  $r_i$ , with  $r_W = 1$  and  $0 < r_C < 1$ , to represent lower reproductive success of aquaculture individuals due to phenotypic changes in behavioral and morphological traits. Combining both wild spawners and cultured escapees of all reproductive age classes, the breeding value distribution of individuals producing age-1 wild-spawned offspring at time  $t$  is

$$n_{W,1,t}^*(g) = \sum_{i \in \{W,C\}} \sum_{x=1}^A r_i b_{i,x} \int n_{i,x,t}(g) P(f|g) \times \exp\left(-\frac{(f-\theta_W)^2}{2S}\right) df \quad (2)$$

given maximum age  $A$ .

Reproduction occurs with random mating, where the encounter probability between parental genotypes  $g_1$  and  $g_2$  is the product of their frequencies in the population. Inheritance follows the infinitesimal model of many unlinked loci contributing additively to the overall genotype, such that offspring genotypes are normally distributed around the mid-parental mean with variance of half the variance at linkage equilibrium  $V_{LE}$  (Turelli and Barton, 1994). The density distribution of newborns is then

$$n_{W,1,t}^{**}(g) = N_{W,1,t}^* \int \frac{\phi_{W,1,t}^*(g_1)\phi_{W,1,t}^*(g_2)}{\sqrt{\pi V_{LE}}} dg_1 dg_2. \quad (3)$$

For simplicity, we do not separately track males and females, and we do not track the parentage (wild, cultured, or hybrid) of progeny of individuals that spawned in the wild. Density dependence occurs among newborns right after hatching, according to the Beverton–Holt function with saturating parameter  $\alpha$  (i.e.,  $1/\alpha$  is the maximum possible density as  $N_{W,1,t}^* \rightarrow \infty$ ). Then the age-1 class distribution dynamics are

$$n_{W,1,t+1}(g) = \frac{n_{W,1,t}^{**}(g)}{1 + \alpha N_{W,1,t}^{**}}. \quad (4)$$

*Density-independent survival and escape.* Assuming the aquaculture population has a constant population size, stable age structure, and constant genetic distribution with mean  $\theta_C$  and variance  $V_C$  dependent on selection in captivity, the aquaculture population at age  $x$  is

$$\tilde{n}_{C,x}(g) = \tilde{N}_{C,x} \frac{1}{\sqrt{2\pi V_C}} \exp\left(-\frac{(g-\theta_C)^2}{2V_C}\right), \quad (5)$$

where  $\tilde{N}_{C,x}$  is the total number of captive individuals at age  $x$ . The aquaculture population in our model only includes fish in the oceanic net pens (the source of escapees) of age 2 to the age of maturation  $x_{mat}$ .

Captive individuals in each age class escape to the wild at proportion  $p_t$  in year  $t$ , and all individuals in the wild (wild-origin and captive escapees from previous years) experience density-independent mortality with age-dependent survival probability  $s_x$ . The wild-origin age classes beyond age-1 now consist of survivors from the previous year, while captive-origin age classes consist of such survivors plus new escapees:

$$n_{W,x+1,t+1}(g) = s_x n_{W,x,t}(g) \quad 1 < x \leq A$$

$$n_{C,x+1,t+1}(g) = \begin{cases} s_x n_{C,x,t}(g) + p_t \tilde{n}_{C,x+1}(g) & 1 < x \leq x_{mat} \\ s_x n_{C,x,t}(g) & x_{mat} < x \leq A. \end{cases} \quad (6)$$

We implement  $p_t$  for different types of escape, keeping the long-term average proportion of escapees at  $p_c$ . For constant spillover, the proportion of escapees  $p_t$  is equal to  $p_c$ , independent of year  $t$ . For pulsed escape,  $p_t$  is set to 1 with probability of  $p_c$ , representing the loss of entire net-pen, and  $p_t = 0$  otherwise. In reality, different types of spillover happen concurrently. We separate these processes on purpose to explore their effects independently.

Note that the reduced spawner success for aquaculture escapees in Eq. (1) can encapsulate a general lower proportion of survivorship and spawning success due to non-genetic effects of rearing in the captive environment, given that all processes between escape and reproduction are linear. The identical age-specific survivorships  $s_x$  for captive and wild fish beyond this eventual proportional reduction means that we assume that the relative survivorships for different ages are the same regardless of the population of origin.

### 2.4. Model implementation and analysis

For computational tractability and efficiency, we simplified the model described above by assuming that the population densities over genotypes in Eqs. (2)–(6) follow normal distributions, and we only keep track of the genetic means, genetic variances, and total population sizes instead of simulating full breeding value distributions (following the analytical approach in Cavalli-Sforza and Feldman, 1976; see SM Appendix A for mathematical details). We base demographic parameters on a life table of Atlantic Salmon (Ryman, 1997) or Atlantic Cod (Kuparinen et al.,

2016); see SM Appendix C for details. As in Table 1, we choose genetic parameters (including a value of  $S$  for strong selection strength) as generic values that lead to significant fitness and demographic effects of aquaculture population on the wild conspecifics, as this is necessary for our central questions to be relevant. In addition, we estimate environmental variance  $E$  relative to the genetic variance at linkage equilibrium  $V_{LE}$  to be in line with the observed heritability data for life history traits (Carlson and Seamons, 2008). This parameterization is analogous to that in Baskett et al. (2013). Based on the data of sampled proportions of aquaculture-origin Atlantic salmon in eastern North American rivers (Morris et al., 2008), we set the population sizes of aquaculture populations to a conservative estimation of 1.5 times the equilibrium size of the wild population in absence of aquaculture, with the long-term average proportion of escapees  $p_c = 0.05$  per year. We also assume the same age structure of the aquaculture population as the equilibrium age class distribution of the wild population without aquaculture interventions. We conducted sensitivity analyses for all relevant parameters to make sure our conclusions on qualitative trends are consistent across parameter values.

We focus our analysis on long-term asymptotic dynamics. First, we iterate the life cycle events described by Eqs. (1)–(6) to equilibrium without aquaculture ( $n_{c,i,t}(g) = 0$ ) after 50 years, then we run the model with constant spillover for 150 years to ensure equilibrium, or with stochastic pulsed spillover to quasi-equilibrium after 300 years (see Fig. D.1 and D.2 in SM Appendix D for sample time series). Our central evaluation metric is the equilibrium mean fitness of the wild population as an indicator of demographically-relevant genetic effects of aquaculture spillover. Trends of population size follow fitness trends (see sample time series in SM Appendix D), but are partially confounded by continual inputs from the aquaculture population. In all cases, we explore how the degree of maladaptation in the aquaculture population influences the outcome by varying the value of the mean aquaculture genotype  $\theta_c$ .

To evaluate how the relative effects of constant versus pulsed spillover depend on the assumption of overlapping versus non-overlapping generations, we compare the equilibrium mean fitness of the wild population in the age-structured model described above to the same metric in the analogous, unstructured model with discrete generations. The unstructured model with non-overlapping generations, fully specified in SM Appendix B, is derived from Baskett et al. (2013) with the same ordering and implementation of demographic events described in Fig. 1, but a time step of simulation represents one generation rather than a year. Therefore, for the unstructured model, we rescale the proportion of escapees in a time step such that it equals to the sum of spillover occurring during a generation time in the age-structured model. We also calculated the lifetime reproductive output from the life table data by summing up the product of age-dependent fecundity and survival probability from age 1 to each age class (see SM Appendix B for mathematical details). We further explore the effect of life history by investigating the overall fitness consequences and consequences of variable spillover for a range of values for generation time and lifetime reproduction for both wild and aquaculture fish.

To evaluate the effect of earlier maturity in aquaculture, we use a different set of age-specific fecundities ( $b_{i,x}$  in Eq. (2)) for escapees. Earlier age at maturity for aquacultured fish can arise from both domestication selection and feeding-driven faster growth (Gjøen, 1997; Gjedrem, 2000). Our model only incorporates the latter non-genetic effect for simplicity and tractability as a first step towards understanding the effect of earlier maturity. This first step can provide insight into whether changing timing of maturity significantly influences expectations for the fitness

consequences of aquaculture escapees and therefore whether further realism that accounts for a genetic basis of this trait, and the associated increase in mathematical complexity and parameters (including genetic covariance between central evolving trait and age at maturity), might be warranted in future modeling efforts. We implement early maturation in the age-structured model by shifting the  $b_x$  values one age-class earlier for the aquaculture population (Bolstad et al., 2017), with all other parameters kept the same (see Table C.2 and C.3 in SM Appendix C for details).

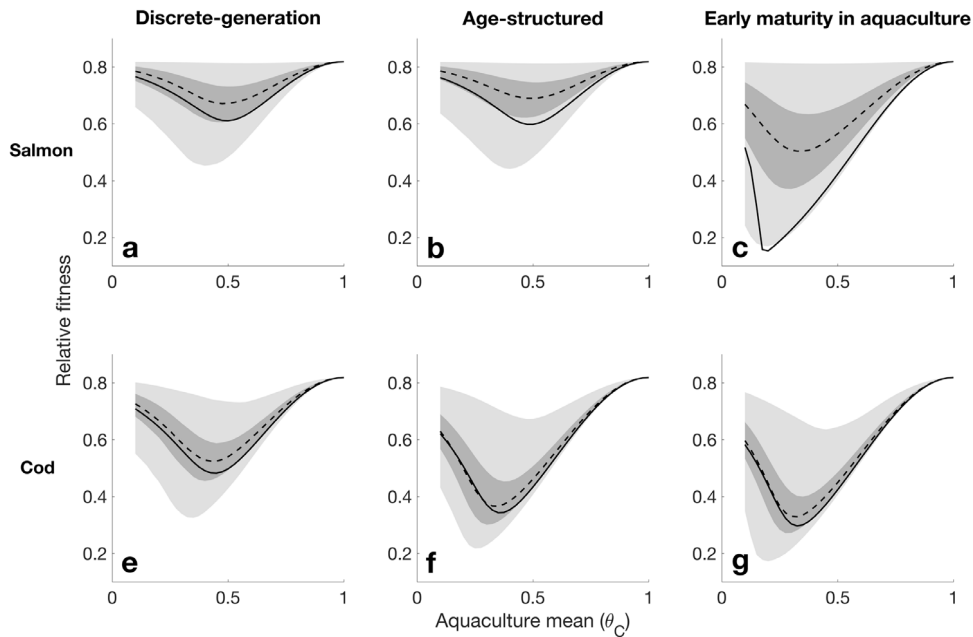
### 3. Results

An intermediate degree of maladaptation ( $\theta_c$ ) can have the greatest fitness and demographic consequences for wild populations as indicated by the fitness trough at intermediate values of  $\theta_c$  in Fig. 2. This result arises from our life cycle ordering where aquaculture spillover occurs after density dependence and escapees experience natural selection before they reproduce in the wild (Baskett et al., 2013). Therefore, extremely maladapted aquaculture escapees are unlikely to survive natural selection to both interbreed with wild individuals and affect the density-dependent mortality of wild individuals. Note that this result does not account for the potential for density-dependent interactions between farmed and wild fish before selection and reproduction (Sundt-Hansen et al., 2015).

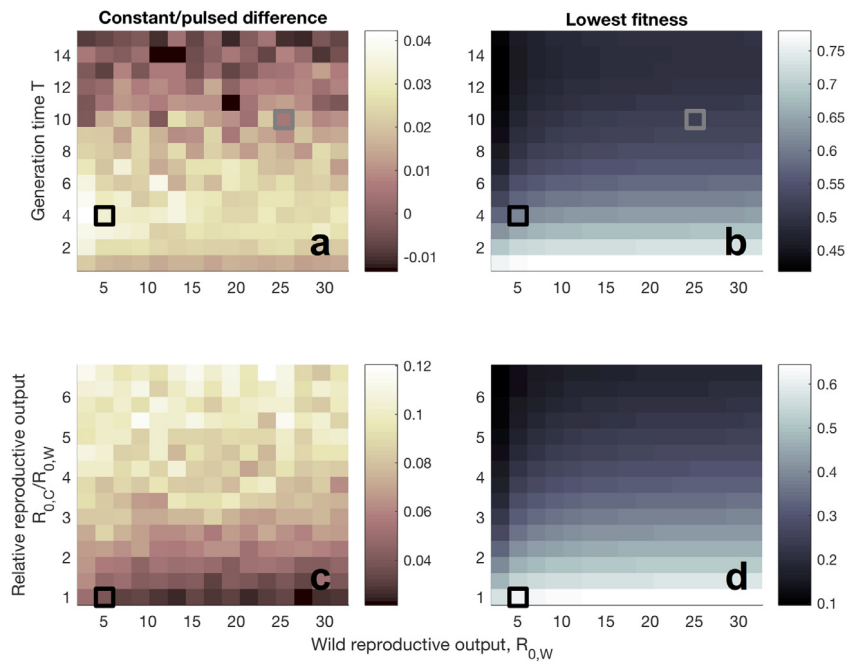
*Age structure and overlapping generations.* To our surprise, implementing age structure does not change the qualitative difference between constant and pulsed escape (compare Fig. 2a versus 2b, 2d versus 2e): the long-term fitness consequences of trickle losses are greater than that of pulsed, large escape events in both the age-structured and unstructured models. Therefore, the averaging effect we expected from age structure and overlapping generations is minor compared to the effect of variability in spillover.

Although age structure does not change the overall qualitative trends for both species modeled here, it causes a greater quantitative effect on cod than salmon, shifting cod's fitness trough to the lower-left corner (compare Fig. 2a versus 2b and 2d versus 2e). In other words, greater fitness effects occur, and occur at a larger difference between aquaculture and wild selection, in the age-structured model of cod compared to the unstructured model. This result arises because the relatively early spawning time compared to the lifespan of cod leads to greater generation overlap in the structured model, which allows escapees to cause greater fitness consequences through more spawning events. Therefore, an analogous proportion of escape events per generation would likely result in analogous outcomes for cod and salmon; here we focus on an analogous absolute number of escape events in total given our goal of accounting for the potential averaging effects of overlapping generations including the potential for a greater escape events per generation with greater generation times.

*Generation time and lifetime fecundity.* To explore the role of life history attributes in determining the fitness consequences of aquaculture escapees beyond the two species modeled here (Fig. 2, first and second columns), we investigated the effect of generation time, lifetime fecundity, and their interaction in the discrete-generation model. In Fig. 3, we compare the differences in fitness between pulsed and constant spillover averaged across  $\theta_c$  (Fig. 3a and c) as well as the lowest fitness across all  $\theta_c$ . The longer the generation time is, the more likely a large pulse of aquaculture spillover happens within a generation, and therefore more escapees affect the population during that generation. Thus, the effect of pulsed, high-level spillover becomes closer to the effect of constant, low-level spillover as the generation time increases (darker colors towards the top in Fig. 3a), with greater



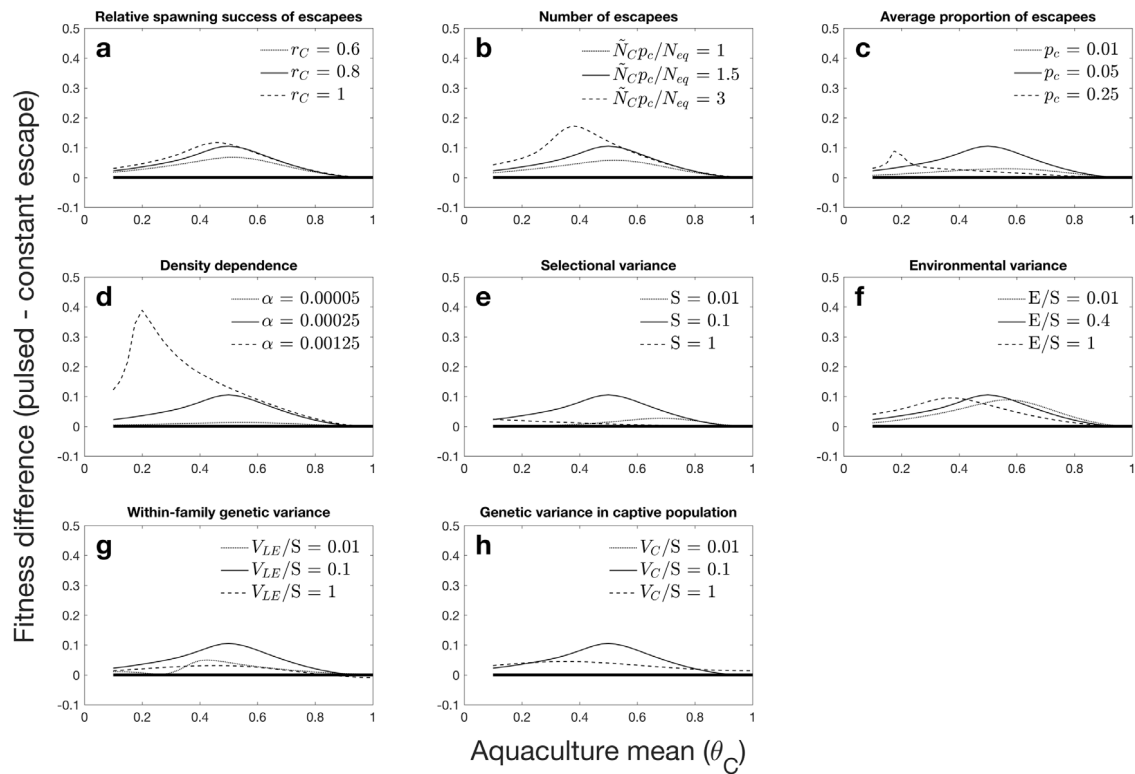
**Fig. 2.** Comparison of the discrete-generation model (first column) to the age-structured model (second column), and the effect of earlier maturity in aquaculture escapees (third column). The first row represents simulation results based on life table of Atlantic salmon and the second row for Atlantic cod. Black, solid lines indicate the outcome given constant, low-level spillover. For the pulsed spillover, the dashed black lines indicate the median outcome, dark gray areas indicate the range between the 25th and 75th percentiles, and light gray areas indicate the range between the 1st and 99th percentiles of the data over multiple runs and generations/years.



**Fig. 3.** The effect of generation time  $T$ , lifetime reproductive output of the wild population  $R_{0,W}$ , and the relative lifetime reproductive output of aquaculture escapees  $R_{0,C}/R_{0,W}$ , on the fitness consequences of aquaculture spillover for wild populations in the discrete-generation model. In the first column (panels a and c), the heatmap indicates the difference in fitness between pulsed, high-level spillover and constant, low-level spillover, plotted as the mean fitness difference averaged over values of  $\theta_c$ . In the second column (b and d), the heatmap indicates the minimum wild fitness value across all  $\theta_c$  values in the model with constant, low-level spillover (corresponding to the y-value of the lowest point in the 'fitness trough'; see Fig. 2 for examples). Darker colors mean a smaller difference between the fitness consequences of pulsed and constant spillover or a smaller worst-case fitness value. For methods of calculating generation time and lifetime reproductive output, see SM Appendix B. Black boxes indicate parameter values for Atlantic salmon, while gray boxes indicate parameter values for Atlantic cod.

fitness consequences (darker colors along the y-axis in Fig. 3b) and fitness consequences occurring at a larger difference in optimal traits (Fig. E.1; i.e., fitness trough shifted downward and to the left). Increasing the lifetime fecundity of aquaculture escapees

( $R_{0,C}$ ), while keeping the lifetime fecundity of wild individuals ( $R_{0,W}$ ) the same, magnifies the difference between the fitness outcomes of pulsed and constant spillover (lighter colors towards the top in Fig. 3c) with greater fitness consequences (Fig. 3 d)



**Fig. 4.** Parameter sensitivity analysis of the fitness difference between pulsed and constant spillovers, analyzed with the age-structured model and life table of Atlantic salmon. The fitness difference is the value of the mean fitness under pulsed, high-level release minus the fitness given constant, low-level leakage. Thick horizontal lines indicate no difference in the fitness consequences of two different settings of escape, and curves above this line correspond to conditions when constant spillover has a greater fitness effect than the pulsed escape. Solid lines indicate default parameter settings (Table 1). Dashed lines correspond to greater values of the targeted parameters, and dotted lines correspond to lower values of the same parameter.

occurring at a larger difference in optima (Fig. E.1; fitness trough shifted downward and to the left) because of the greater relative contribution of maladaptive individuals. The larger number of aquaculture individuals escaping to the wild at once for pulsed spillover further amplifies this effect. However, changing the lifetime reproductive output of wild individuals has little effect on the fitness outcome (Fig. 3), as density dependence eventually limits the relative contribution of wild-origin individuals in our model.

**Earlier maturity.** Assuming earlier maturity in aquaculture while keeping other life history parameters unchanged in the age-structured model, greater fitness effects occur, and occur at a larger fitness difference (smaller  $\theta_c$ ) between aquaculture and wild selection for salmon (fitness trough shifting downward and to the left; Fig. 2b, c), but less so for cod (see below). In addition, earlier maturity causes a greater difference between constant versus pulsed aquaculture spillovers (Fig. 2b, c). Analysis of differential maturation in the wild and aquaculture allows us to separate the effect of spawning schedule from other factors such as longevity and overlapping generations in an age-structured model. Assuming that aquaculture escapees mature and reproduce earlier than wild-origin individuals is in effect similar to setting a higher relative spawning success  $r_c$  of escapees (Fig. 4a) or higher relative lifetime fecundity of aquaculture individuals  $R_{0,c}/R_{0,w}$  in the discrete-generation model (Fig. 3c, d), all of which lead to greater fitness consequences of aquaculture escapees overall and larger discrepancies between pulsed and constant spillovers for Atlantic salmon.

In contrast, earlier maturity of aquaculture individuals by 1 year has a negligible effect on predictions for cod (Fig. 2e, f). Because the cod can survive up to 20 years in the wild, the

shift of reproduction schedule by only 1 year makes little difference in the lifetime reproductive output of aquaculture escapees (an increase of 20% for cod versus 513% for salmon). In other words, when assuming an equal magnitude of shifts in fecundity schedule, aquaculture escapees have a greater effect on wild population for species with shorter life span, especially in the case of constant, low-level leakage. Note that an equal proportional effect on the timing of maturity (e.g., 5 years for cod as compared to 1 year for salmon) would likely result in a similar outcome across species, but such large shifts in the timing of maturity for longer-lived species are unlikely to be biologically relevant.

**Parameter sensitivity analysis.** In Fig. 4, we evaluate the sensitivity of our key result to parameter values. The result that constant, low-level spillover has a greater average effect on the fitness of wild population compared with pulsed, high-level spillover is robust across a wide range of parameter values, illustrated in Fig. 4 by the fitness difference between these two simulations remaining positive (above the thick horizontal line) through the parameter ranges explored. Decreasing the relative success (Fig. 4a), total number (Fig. 4b), and proportion over time (Fig. 4c) of aquaculture escapees all lead to a smaller difference between constant and pulsed spillovers, as does decreasing the strength of competition (Fig. 4d). All of these changes represent a smaller demographic influence of aquaculture escapees on the wild population, and therefore a smaller fitness effect overall. Intermediate values of selection strength (Fig. 4e), environmental variance (Fig. 4f), and genetic variance (Fig. 4g, h) lead to the greatest fitness differences between constant and pulsed spillover. This is because at one extreme of these values, evolution is rapid enough for fitness consequences to be minimal; whereas at the other extreme, slow evolution causes the fitness dynamics of the pulsed spillover to approach those of the constant spillover.



#### 4. Discussion

Our results indicate that aquaculture escapees can have substantial demographic and fitness effects on wild population, especially at intermediate level of genetic divergence between cultured and wild individuals and with strong selection (Fig. 2), as occurs in models with a variety of genetic and demographic representations and parameterizations of spillover from both aquaculture and hatcheries (e.g., Hutchings, 1991; Fleming, 1995; Tufto, 2001, 2010; Lorenzen, 2005; Hindar et al., 2006; Liu et al., 2013; Baskett et al., 2013; Castellani et al., 2018). We expand this theory by showing the role of life history attributes of the focal species in determining the long-term fitness outcome. Specifically, species with long generation times might experience greater fitness consequences from aquaculture escapees, whereas species with shorter generation times are more sensitive to the stochastic effects of spillover and life history changes of escapees (i.e., earlier maturity; Figs. 2 and 3). Consistent with (Baskett et al., 2013), our analysis on the variable spillover of aquaculture fish suggest that continuous, small-scale escape events can cause greater fitness consequences on the wild fish compared to large pulses of spillover, even with the averaging effect of overlapping generations (Fig. 2). Although we focus on two iteroparous species for model parameterization and analysis, the unstructured model approximately captures the life cycle of a semelparous species (e.g., Pacific salmon), for which the same conclusion holds here and in Baskett et al. (2013). Furthermore, this finding for our model of commercial aquaculture is analogous to the expectation in conservation hatcheries that short-term releases can reduce evolutionary risks as compared to long-term continuous releases (McClure et al., 2008).

Expanding on a variety of existing models that demonstrate that stochasticity in migration rates can enhance genetic divergence and local adaptation (e.g., Fife and Peletier, 1981; Lenormand and Raymond, 2000; Rice and Papadopoulos, 2009; Rice et al., 2011), our model showed the robustness of the outcome of constant versus variable gene flow to a wide variety of assumptions and parameter values. Therefore, stochastic dispersal is an additional mechanism that can explain observations of genetic divergence at local spatial scales with high migration rates, typically explained by sexual selection against migrants, post-zygotic selective barriers, and monopolization effects (reviewed by Richardson et al., 2014). Even when the migrants have considerable chances of surviving and reproducing in the new environment, high variance in migration rates can lead to maintenance of local genetic adaptation by allowing natural selection to act during the intervals between migration events. Such processes might be most relevant to systems where dispersal is both stochastic and substantial, such as wind-dispersed seeds (Nathan and Muller-Landau, 2000; Levin, 1988) and planktonic marine larvae (Hogan et al., 2012). In addition to this potential effect of stochastic recruitment on local adaptation, theory indicates that temporal variability in dispersal rates might promote meta-population persistence (Williams and Hastings, 2013), increase range limits of marine species (Gaylord and Gaines, 2000), and accelerate the spread of invasive species (Ellner and Schreiber, 2012). Therefore, stochastic dispersal may have an under-appreciated role in eco-evolutionary dynamics in general.

**Model assumptions.** As with any model, we make a number of simplifying assumptions for tractability. First, a major assumption of our model is to keep the same average number of aquaculture escapees over time for pulsed and constant spillover. As in Baskett et al. (2013), we made this assumption for standardized comparison between different types of spillover. However, in situations where the higher variability is also associated with higher average migration rates over time, our previous conclusion might not

apply. In reality, the aquaculture escapees are likely to escape through a combination of constant and pulsed spillover (Morris et al., 2008), which results in stochastic fitness consequences on a continuum between the two extremes. Second, we assume a specific life cycle ordering of selection–reproduction–density-dependent survival–density-independent survival–escape. In Baskett et al. (2013), we found that selection right after escape (as in our model) would reduce the effects of aquaculture escapees before they can reproduce, whereas having escape events happen before density-dependent survival would lead to a greater fitness effect because hybrids can competitively displace wild individuals. In reality, selection occurs at multiple stages, further complicating the effect of relative ordering of life cycle events. Third, we ignore demographic stochasticity and genetic drift, which could particularly affect small wild populations after a large pulse event, and therefore might have underestimated the effects of variable spillover. Fourth, we assume a genetic architecture of many genes of small effect; incorporating genes of major and minor effect could increase the rate of trait change, which would increase the potential for reduced fitness consequences under variable spillover.

The effect of earlier maturation in aquaculture might depend on several dynamics ignored for simplicity. First, earlier maturity in captivity might be genetically heritable (Lorenzen et al., 2012; Bolstad et al., 2017) and passed to the wild population through introgression, which would increase the fitness effects of escapees as well as decrease the generation time of the wild population. However, because of its dependence on environmentally-driven growth and survival, species often exhibit considerable phenotypic plasticity in this trait (Schlichting and Pigliucci, 1998). Furthermore, earlier-maturing fish might experience earlier mortality (Beverton et al., 2004) or lower future fecundity (Fleming and Petersson, 2001), which would reduce the fitness effects of aquaculture escapees. At the same time, environmental-caused earlier maturation in captivity might be lost when the fish escape into the wild, which would also reduce the impacts of escapees. Given the impact of earlier maturity found here, more realistic models that mechanistically account for both the genetic and plastic effects of aquaculture rearing on the timing of maturity and its demographic consequences would be necessary to fully quantify the fitness consequences of aquaculture escapees, especially for shorter-lived species.

**Management implications.** While we expect greater fitness consequences of aquaculture escapees for longer-lived species (e.g., Atlantic cod), domestication effects that shorten generation time (e.g., higher mortality, shorter longevity and/or delayed, lower fecundity) will reduce those consequences. Our model predicts that species with shorter generation times (e.g., Atlantic salmon) are more sensitive to the effects of variable spillover, such that devoting more resources to controlling small-scale escape events could help achieve a goal of minimizing the fitness consequences of aquaculture escapees. However, we currently have very limited knowledge about the magnitude of trickle losses of aquaculture fish because such small-scale events are harder to detect and often unreported. Thus, more monitoring efforts are needed (e.g. using biomarkers, Arechavala-Lopez et al., 2016) to verify our modeling assumptions and results, as well as to design the optimal management strategies. A further action that our model suggests might reduce unintended fitness consequences is delaying sexual maturation in aquaculture, which can also be economically beneficial because the size of fish at maturity for harvest is positively related to their expected age of first reproduction (Hutchings and Fraser, 2008). Given the recent discovery of a single locus that strongly controls the age at maturity in salmon (Barson et al., 2015), it might be possible in the future to efficiently select for late-maturing fish in aquaculture.

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## Appendix

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## References

- Arechavala-Lopez, P., Milošević-González, M., Sanchez-Jerez, P., 2016. Using trace elements in otoliths to discriminate between wild and farmed European sea bass (*Dicentrarchus labrax* L.) and gilthead sea bream (*Sparus aurata* L.). *Int. Aquatic Res.* 8 (3), 263–273. <http://dx.doi.org/10.1007/s40071-016-0142-1>.
- Barson, N.J., Aykanat, T., Hindar, K., Baranski, M., Bolstad, G.H., Fiske, P., Jacq, C., Jensen, A.J., Johnston, S.E., Karlsson, S., et al., 2015. Sex-dependent dominance at a single locus maintains variation in age at maturity in salmon. *Nature* 528 (7582), 405–408. <http://dx.doi.org/10.1038/nature16062>.
- Baskett, M.L., Burgess, S.C., Waples, R.S., 2013. Assessing strategies to minimize unintended fitness consequences of aquaculture on wild populations. *Evol. Appl.* 6 (7), 1090–1108. <http://dx.doi.org/10.1111/eva.12089>.
- Bekkevold, D., Hansen, M.M., Nielsen, E.E., 2006. Genetic impact of gaidoid culture on wild fish populations: predictions, lessons from salmonids, and possibilities for minimizing adverse effects. *ICES J. Mar. Sci.* 63 (2), 198–208. <http://dx.doi.org/10.1016/j.icesjms.2005.11.003>.
- Beverton, R.J., Hylan, A., Østvedt, O.J., Alvsvaag, J., Iles, T.C., 2004. Growth, maturation, and longevity of maturation cohorts of Norwegian spring-spawning herring. *ICES J. Mar. Sci.* 61 (2), 165–175. <http://dx.doi.org/10.1016/j.icesjms.2004.01.001>.
- Bolstad, G.H., Hindar, K., Robertsen, G., Jonsson, B., Sægrov, H., Diserud, O.H., Fiske, P., Jensen, A.J., Urdal, K., Næsje, T.F., Barlaup, B.T., Florø-Larsen, B., Lo, H., Niemelä, E., Karlsson, S., 2017. Gene flow from domesticated escapes alters the life history of wild Atlantic salmon. *Nat. Ecol. Evol.* 1, 124. <http://dx.doi.org/10.1038/s41559-017-0124>.
- Carlson, S.M., Seamons, T.R., 2008. A review of quantitative genetic components of fitness in salmonids: implications for adaptation to future change. *Evol. Appl.* 1 (2), 222–238. <http://dx.doi.org/10.1111/j.1752-4571.2008.00025.x>.
- Castellani, M., Heino, M., Gilbey, J., Araki, H., Svendsen, T., Glover, K.A., 2018. Modeling fitness changes in wild Atlantic salmon populations faced by spawning intrusion of domesticated escapees. *Evol. Appl.* 11 (6), 1010–1025. <http://dx.doi.org/10.1111/eva.12615>.
- Cavalli-Sforza, L., Feldman, M., 1976. Evolution of continuous variation: direct approach through joint distribution of genotypes and phenotypes. *Proc. Natl. Acad. Sci.* 73 (5), 1689–1692.
- DFO, 2017. Reporting escapes. URL: <http://www.dfo-mpo.gc.ca/aquaculture/protect-protege/escape-prevention-evasions-eng.html>, (Accessed 18.02.18).
- Ellner, S.P., Schreiber, S.J., 2012. Temporally variable dispersal and demography can accelerate the spread of invading species. *Theor. Popul. Biol.* 82 (4), 283–298. <http://dx.doi.org/10.1016/j.tpb.2012.03.005>.
- FAO, 2004. Cultured aquatic species information programme (CASIP). In: FAO Fisheries and Aquaculture Department [Online]. Rome.
- FAO, 2016. The State of World Fisheries and Aquaculture 2016. Rome, p. 200.
- Fife, P., Peletier, L., 1981. Clines induced by variable selection and migration. *Proc. R. Soc. Lond. B* 214 (1194), 99–123. <http://dx.doi.org/10.1098/rspb.1981.0084>.
- Fleming, I.A., 1995. Reproductive success and the genetic threat of cultured fish to wild populations. In: Philipp, D.P., Epifanio, J.M., Marsden, J.E., Claussen, J.E. (Eds.), *Protection of Aquatic Biodiversity. Proceedings of the World Fisheries Congress, Theme 3*. Oxford and IBH Publishing CO. PVT. LTD, pp. 117–135.
- Fleming, I., Petersson, E., 2001. The ability of released, hatchery salmonids to breed and contribute to the natural productivity of wild populations. *Nordic J. Freshw. Res.* 71–98.
- Ford, J.S., Myers, R.A., 2008. A global assessment of salmon aquaculture impacts on wild salmonids. *PLoS Biol.* 6 (2), 0411–0417. <http://dx.doi.org/10.1371/journal.pbio.0060033>.
- Frankham, R., 2008. Genetic adaptation to captivity in species conservation programs. *Mol. Ecol.* 17 (1), 325–333. <http://dx.doi.org/10.1111/j.1365-294X.2007.03399.x>.
- Fraser, D.J., Houde, A.L.S., Debes, P.V., O'Reilly, P., Eddington, J.D., Hutchings, J.A., 2010. Consequences of farmed-wild hybridization across divergent wild populations and multiple traits in salmon. *Ecol. Appl.* 20 (4), 935–953. <http://dx.doi.org/10.1890/09-0694.1>.
- Froese, R., Pauly, D. (Eds.), 2018. FishBase. URL: [www.fishbase.org](http://www.fishbase.org), (Accessed 27.08.18).
- Gaylord, B., Gaines, S.D., 2000. Temperature or transport? range limits in marine species mediated solely by flow. *Amer. Nat.* 155 (6), 769–789. <http://dx.doi.org/10.1086/303357>.
- Gjedrem, T., 2000. Genetic improvement of cold-water fish species. *Aquac. Res.* 31 (1), 25–33. <http://dx.doi.org/10.1046/j.1365-2109.2000.00389.x>.
- Gjøen, H., 1997. Past, present, and future of genetic improvement in salmon aquaculture. *ICES J. Mar. Sci.* 54 (6), 1009–1014. [http://dx.doi.org/10.1016/S1054-3139\(97\)80005-7](http://dx.doi.org/10.1016/S1054-3139(97)80005-7).
- Glover, K.A., Otterå, H., Olsen, R.E., Slinde, E., Taranger, G.L., Skaala, Ø., 2009. A comparison of farmed, wild and hybrid Atlantic salmon (*Salmo salar* L.) reared under farming conditions. *Aquaculture* 286 (3), 203–210. <http://dx.doi.org/10.1016/j.aquaculture.2008.09.023>.
- Glover, K.A., Solberg, M.F., McGinnity, P., Hindar, K., Verspoor, E., Coulson, M.W., Hansen, M.M., Araki, H., Skaala, Ø., Svendsen, T., 2017. Half a century of genetic interaction between farmed and wild Atlantic salmon: Status of knowledge and unanswered questions. *Fish Fish.* 18 (5), 890–927. <http://dx.doi.org/10.1111/faf.12214>.
- Hansen, L.P., Windsor, M.L., 2006. Interactions between aquaculture and wild stocks of Atlantic salmon and other diadromous fish species: Science and management, challenges and solutions. an introduction by the conveners. *ICES J. Mar. Sci.* 63 (7), 1159–1161. <http://dx.doi.org/10.1016/j.icesjms.2006.05.003>.
- Hindar, K., Fleming, I.A., McGinnity, P., Diserud, O., 2006. Genetic and ecological effects of salmon farming on wild salmon: modelling from experimental results. *ICES J. Mar. Sci.* 63 (7), 1234–1247. <http://dx.doi.org/10.1016/j.icesjms.2006.04.025>.
- Hindar, K., Ryman, N., Utter, F., 1991. Genetic effects of cultured fish on natural fish populations. *Can. J. Fish. Aquat. Sci.* 48 (5), 945–957. <http://dx.doi.org/10.1139/f91-111>.
- Hogan, J.D., Thiessen, R.J., Sale, P.F., Heath, D.D., 2012. Local retention, dispersal and fluctuating connectivity among populations of a coral reef fish. *Oecologia* 168 (1), 61–71. <http://dx.doi.org/10.1007/s00442-011-2058-1>.
- Hutchings, J.A., 1991. The threat of extinction to native populations experiencing spawning intrusions by cultured Atlantic salmon. *Aquaculture* 98 (1–3), 119–132. [http://dx.doi.org/10.1016/0044-8486\(91\)90377-j](http://dx.doi.org/10.1016/0044-8486(91)90377-j).
- Hutchings, J.A., Fraser, D.J., 2008. The nature of fisheries- and farming-induced evolution. *Mol. Ecol.* 17 (1), 294–313. <http://dx.doi.org/10.1111/j.1365-294X.2007.03485.x>.
- Jackson, D., Drumm, A., McEvoy, S., Jensen, Ø., Mendiola, D., Gabiña, G., Borg, J.A., Papageorgiou, N., Karakassis, Y., Black, K.D., 2015. A pan-European valuation of the extent, causes and cost of escape events from sea cage fish farming. *Aquaculture* 436, 21–26. <http://dx.doi.org/10.1016/j.aquaculture.2014.10.040>.
- Jensen, Ø., Dempster, T., Thorstad, E.B., Uglem, I., Fredheim, A., 2010. Escapes of fishes from Norwegian sea-cage aquaculture: causes, consequences and prevention. *Aquac. Environ. Interact.* 1 (1), 71–83. <http://dx.doi.org/10.3354/aei00008>.
- Jonsson, B., Jonsson, N., 2006. Cultured Atlantic salmon in nature: a review of their ecology and interaction with wild fish. *ICES J. Mar. Sci.* 63 (7), 1162–1181. <http://dx.doi.org/10.1016/j.icesjms.2006.03.004>.
- Karlsson, S., Diserud, O.H., Fiske, P., Hindar, K., editor: W. Stewart Grant, H., 2016. Widespread genetic introgression of escaped farmed Atlantic salmon in wild salmon populations. *ICES J. Mar. Sci.* 73, 2488–2498. <http://dx.doi.org/10.1093/icesjms/fsw121>.
- Kuparinen, A., Hutchings, J.A., Waples, R.S., 2016. Harvest-induced evolution and effective population size. *Evol. Appl.* 9 (5), 658–672. <http://dx.doi.org/10.1111/eva.12373>.
- Laike, L., Schwartz, M.K., Waples, R.S., Ryman, N., 2010. Compromising genetic diversity in the wild: Unmonitored large-scale release of plants and animals. *Trends Ecol. Evol.* 25 (9), 520–529. <http://dx.doi.org/10.1016/j.tree.2010.06.013>.
- Lenormand, T., Raymond, M., 2000. Analysis of clines with variable selection and variable migration. *Amer. Nat.* 155 (1), 70–82. <http://dx.doi.org/10.1086/303295>.
- Levin, D.A., 1988. Consequences of stochastic elements in plant migration. *Amer. Nat.* 132 (5), 643–651. <http://dx.doi.org/10.1086/284879>.

- Liu, Y., Diserud, O.H., Hindar, K., Skonhøft, A., 2013. An ecological-economic model on the effects of interactions between escaped farmed and wild salmon (*salmo salar*). *Fish Fish.* 14 (2), 158–173. <http://dx.doi.org/10.1111/j.1467-2979.2012.00457.x>.
- Lorenzen, K., 2005. Population dynamics and potential of fisheries stock enhancement: practical theory for assessment and policy analysis. *Philos. Trans. R. Soc. B* 360 (1453), 171–189. <http://dx.doi.org/10.1098/rstb.2004.1570>.
- Lorenzen, K., Beveridge, M.C., Mangel, M., 2012. Cultured fish: integrative biology and management of domestication and interactions with wild fish. *Biol. Rev.* 87 (3), 639–660. <http://dx.doi.org/10.1111/j.1469-185X.2011.00215.x>.
- Lynch, M., O'Hely, M., 2001. Captive breeding and the genetic fitness of natural populations. *Conserv. Genet.* 2 (4), 363–378. <http://dx.doi.org/10.1023/A:1012550620717>.
- McClure, M.M., Utter, F.M., Baldwin, C., Carmichael, R.W., Hassemer, P.F., Howell, P.J., Spruell, P., Cooney, T.D., Schaller, H.A., Petrosky, C.E., 2008. Evolutionary effects of alternative artificial propagation programs: implications for viability of endangered anadromous salmonids. *Evol. Appl.* 1 (2), 356–375. <http://dx.doi.org/10.1111/j.1752-4571.2008.00034.x>.
- McGinnity, P., Prodöhl, P., Ferguson, A., Hynes, R., Maoiléidigh, N.ó., Baker, N., Cotter, D., O'Hea, B., Cooke, D., Rogan, G., Taggart, J., Cross, T., 2003. Fitness reduction and potential extinction of wild populations of Atlantic salmon, *Salmo salar*, as a result of interactions with escaped farm salmon. *Proc. R. Soc. Lond. B* 270 (1532), 2443–2450. <http://dx.doi.org/10.1098/rspb.2003.2520>.
- Moe, H., Dempster, T., Sunde, L.M., Winther, U., Fredheim, A., 2007. Technological solutions and operational measures to prevent escapes of Atlantic cod (*Gadus morhua*) from sea cages. *Aquac. Res.* 38 (1), 91–99. <http://dx.doi.org/10.1111/j.1365-2109.2006.01638.x>.
- Morris, M.R., Fraser, D.J., Heggelin, A.J., Whoriskey, F.G., Carr, J.W., O'Neil, S.F., Hutchings, J.A., 2008. Prevalence and recurrence of escaped farmed Atlantic salmon (*Salmo salar*) in eastern North American rivers. *Can. J. Fish. Aquat. Sci.* 65 (12), 2807–2826. <http://dx.doi.org/10.1139/F08-181>.
- Myers, R.A., 2001. Stock and recruitment: generalizations about maximum reproductive rate, density dependence, and variability using meta-analytic approaches. *ICES J. Mar. Sci.* 58 (5), 937–951. <http://dx.doi.org/10.1006/jmsc.2001.1109>.
- Nathan, R., Muller-Landau, H.C., 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends Ecol. Evol.* 15 (7), 278–285. [http://dx.doi.org/10.1016/S0169-5347\(00\)01874-7](http://dx.doi.org/10.1016/S0169-5347(00)01874-7).
- Naylor, R., Hindar, K., Fleming, I.A., Goldberg, R., Williams, S., Volpe, J., Whoriskey, F., Eagle, J., Kelso, D., Mangel, M., 2005. Fugitive salmon: Assessing the risks of escaped fish from net-pen aquaculture. *BioScience* 55 (5), 427–437. [http://dx.doi.org/10.1641/0006-3568\(2005\)055\[0427:fsatro\]2.0.co;2](http://dx.doi.org/10.1641/0006-3568(2005)055[0427:fsatro]2.0.co;2).
- Norwegian Directorate of Fisheries, 2017. Statistics on escapes, URL: <https://www.fiskeridir.no/Akvakultur/Statistikk-akvakultur/Roemningsstatistikk>, (Accessed 18.02.18).
- Norwegian Institute for Nature Research (NINA), 2018. Status of wild Atlantic salmon in Norway 2018, URL <https://www.vitenskapsradet.no/Nyheter/Nyhetsartikkel/ArticleId/4559/Status-of-wild-Atlantic-salmon-in-Norway-2018>, (Accessed 11.09.18).
- Rhymer, J.M., Simberloff, D., 1996. Extinction by hybridization and introgression. *Annu. Rev. Ecol. Syst.* 27 (1), 83–109. <http://dx.doi.org/10.1146/annurev.ecolsys.27.1.83>.
- Rice, S.H., Papadopoulos, A., 2009. Evolution with stochastic fitness and stochastic migration. *PLoS One* 4 (10), e7130. <http://dx.doi.org/10.1371/journal.pone.0007130>.
- Rice, S.H., Papadopoulos, A., Harting, J., 2011. Evolutionary biology – concepts, biodiversity, macroevolution and genome evolution. In: *Evolutionary Biology – Concepts, Biodiversity, Macroevolution and Genome Evolution*. Springer, Berlin, Heidelberg, pp. 21–33. <http://dx.doi.org/10.1007/978-3-642-20763-1>.
- Richardson, J.L., Urban, M.C., Bolnick, D.I., Skelly, D.K., 2014. Microgeographic adaptation and the spatial scale of evolution. *Trends Ecol. Evol.* 29 (3), 165–176. <http://dx.doi.org/10.1016/j.tree.2014.01.002>.
- Ronce, O., Kirkpatrick, M., 2001. When Sources Become Sinks: Migrational Meltdown In heterogeneous Habitats. *Evolution* 55 (8), 1520–1531. <http://dx.doi.org/10.1111/j.0014-3820.2001.tb00672.x>.
- Ryman, N., 1997. Minimizing adverse effects of fish culture: understanding the genetics of populations with overlapping generations. *ICES J. Mar. Sci.* 54 (6), 1149–1159. [http://dx.doi.org/10.1016/S1054-3139\(97\)80021-5](http://dx.doi.org/10.1016/S1054-3139(97)80021-5).
- Schlichting, C., Pigliucci, M., 1998. *Phenotypic Evolution: A Reaction Norm Perspective*. Sinauer.
- Skilbrei, O.T., Heino, M., Svåsand, T., 2014. Using simulated escape events to assess the annual numbers and destinies of escaped farmed Atlantic salmon of different life stages from farm sites in Norway. *ICES J. Mar. Sci.* 72 (2), 670–685. <http://dx.doi.org/10.1093/icesjms/fsu133>.
- Sundt-Hansen, L., Huisman, J., Skoglund, H., Hindar, K., 2015. Farmed Atlantic salmon *salmo salar* L. parr may reduce early survival of wild fish. *J. Fish Biol.* 86 (6), 1699–1712. <http://dx.doi.org/10.1111/jfb.12677>.
- Thorpe, J., 1991. Acceleration and deceleration effects of hatchery rearing on salmonid development, and their consequences for wild stocks. *Aquaculture* 98 (1–3), 111–118. [http://dx.doi.org/10.1016/0044-8486\(91\)90376-1](http://dx.doi.org/10.1016/0044-8486(91)90376-1).
- Thorpe, J., 2004. Life history responses of fishes to culture. *J. Fish Biol.* 65, 263–285. <http://dx.doi.org/10.1111/j.0022-1112.2004.00556.x>.
- Tufto, J., 2001. Effects of releasing maladapted individuals: a demographic-evolutionary model. *Amer. Nat.* 158 (4), 331–340. <http://dx.doi.org/10.1086/321987>.
- Tufto, J., 2010. Gene flow from domesticated species to wild relatives: Migration load in a model of multivariate selection. *Evolution* 64 (1), 180–192. <http://dx.doi.org/10.1111/j.1558-5646.2009.00807.x>.
- Tufto, J., 2017. Domestication and fitness in the wild: A multivariate view. *Evolution* 71 (9), 2262–2270. <http://dx.doi.org/10.1111/evo.13307>.
- Turelli, M., Barton, N., 1994. Genetic and statistical analyses of strong selection on polygenic traits: what, me normal?. *Genetics* 138 (3), 913–941.
- Uglem, I., Bjørn, P.A., Dale, T., Kerwath, S., Økland, F., Nilsen, R., Aas, K., Fleming, I., McKinley, R.S., 2008. Movements and spatiotemporal distribution of escaped farmed and local wild Atlantic cod (*Gadus morhua* L.). *Aquac. Res.* 39 (2), 158–170. <http://dx.doi.org/10.1111/j.1365-2109.2007.01872.x>.
- Waples, R.S., Hindar, K., Hard, J.J., 2012. Genetic risks associated with marine aquaculture, NOAA Tech. Memo. NMFS-NWFSC-119, U.S. Dept. of Commerce.
- Waples, R.S., Luikart, G., Faulkner, J.R., Tallmon, D.A., 2013. Simple life-history traits explain key effective population size ratios across diverse taxa. *Proc. R. Soc. B* 280 (1768), <http://dx.doi.org/10.1098/rspb.2013.1339>, 20131339–20131339.
- Weir, L.K., Grant, J.W., 2005. Effects of aquaculture on wild fish populations: a synthesis of data. *Environ. Rev.* 13 (4), 145–168. <http://dx.doi.org/10.1139/a05-012>.
- Williams, P.D., Hastings, A., 2013. Stochastic dispersal and population persistence in marine organisms. *Amer. Nat.* 182 (2), 271–282. <http://dx.doi.org/10.1086/671059>.