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by Erin S. Dunlop, Anne Maria Eikeset, and Nils Chr. Stenseth

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Eco-evolutionary Model Description

We built an individual-based eco-evolutionary (also referred to as an eco-genetic) model (Dunlop et al. 2009) which, except for its parameterization (Table A1), closely follows a previous model (Dunlop et al. 2007). The model also closely follows a previous model parameterized for Atlantic cod *Gadus morhua*, except that the previous model included additional evolving traits (Dunlop et al. 2009). Our model follows the evolution of a linear probabilistic maturation reaction norm (PMRN), which is described by two quantitative traits: the slope and intercept. We chose to model the PMRN because it allows the inclusion of phenotypic plasticity in the maturation process (Heino et al. 2002), is under genetic control (Reznick 1993), is predicted to undergo evolution in response to harvest (Dunlop et al. 2007, 2009), and has undergone dramatic shifts towards earlier ages and smaller sizes at maturation in

many commercially harvested populations (Jørgensen et al. 2007). We used basic quantitative genetics theory (Falconer and Mackay 1996) to represent the variance structure, inheritance, and phenotypic expression of our genetically-based PMRN. As such, offspring inherited the PMRNs of their parents from a normal distribution with mean equal to the mid-parental value and variance σ_0^2 ; the later is held constant through time at half the genetic variance σ_G^2 of the initial population, $\sigma_0^2 = 0.5\sigma_G^2$ (Dunlop et al. 2009). The phenotypic expression σ_p^2 of genetic traits was also determined from a Gaussian function with mean equal to the individual's genetic trait value and a constant environmental variance σ_E^2 , the later calculated by assuming a conservative heritability h^2 of 0.2 in the initial population ($\sigma_E^2 = \sigma_G^2(h^{-2} - 1)$). Individuals were assigned trait values in the initial population assuming a coefficient of genetic variation $CV_G = 100\sqrt{\sigma_G^2} / \bar{T}$ and a mean trait value \bar{T} , where $\bar{T} = \bar{i}_G$ for the PMRN intercept and $\bar{T} = \bar{s}_G$ for the PMRN slope. An individual's probability to mature at a given age a was estimated by their PMRN midpoint l_{p50} , body size l_a and a logistic function,

$$P_m = \frac{1}{1 + e^{-(l_a - l_{p50})/q}},$$

where $q = W / [\text{logit}(p_u) - \text{logit}(p_l)]$, $\text{logit}(p) = \ln(p/(1-p))$, and p_u and p_l are the probabilities, 0.01 and 0.99 respectively, of the upper and lower bounds of the PMRN width W (see Heino et al. 2002 for a description of the PMRN width). An individual's somatic growth was density-dependent, declining as the population biomass b increased,

$$g_d = \frac{\beta}{1 + (\alpha b)^\delta},$$

where β is the growth rate when biomass equals zero (i.e., the maximum growth rate). To calculate the population biomass, length of an individual is first converted to units of mass (w) assuming a simple allometric relationship $w_a = \nu l_a^\gamma$. An individual's lifetime phenotypic growth was then described by the Lester et al. growth model (Lester et al. 2004) where length growth is linear and equal to g_d prior to maturation and asymptotic as a function of reproductive investment R after maturation. Reproduction occurs between random pairs of mature individuals after the growing season. The fecundity per pair is determined from an allometric relationship with body length, $f = \varepsilon L_a^b$ with the mother chosen randomly from the pair. The number of recruits surviving their first year was calculated from a Beverton-Holt stock recruitment relationship (Hilborn and Walters 1992),

$$N_r = \frac{\partial f_T}{1 + \mu f_T},$$

where f_T is the total population fecundity. The survival probability applied to each reproductive pair's fecundity was then calculated as N_r / f_T . Annually, there was a constant natural mortality probability applied separately to immature (M_I) and mature (M_A) fish. The mortality of mature fish was set higher than that of immature fish to account for the cost of reproduction (Dunlop et al. 2007). The model was updated at discrete, annual time-steps and the genetic trait values (i.e., the slope and intercept of the PMRN), body length, age, and maturation status were tracked each year for all individuals in the population. The model was run for 100 years prior to the introduction of harvesting in order to allow the population to reach demographic and evolutionary equilibrium. Fishing was then implemented for 100 years at a given harvest rate, followed by 100 years of a harvest moratorium.

The average lifetime reproductive output of females in a cohort, R_0 , was estimated directly from our individual-based model. This was done by tracking, for each female, the number of offspring that reach sexual maturity and then calculating the average number per cohort. For each cohort we calculated the population growth rate r , as $r = \ln[R_0]/G$ where G is the generation time, here estimated as the mean age at maturation for the cohort (Kuparinen and Hutchings 2012). Our approach to estimating population growth rate from R_0 is by choice simple. The generation time was estimated from age at maturation, which is a simplification because our modeled population contains overlapping generations (Krebs 1994). Our model should also be extended in the future to consider additional evolving traits and different harvesting selectivities, which can impact the population's evolutionary response to harvest (Dunlop et al. 2009) and therefore might alter predictions for r . Similarly, additional features of a species life history, such as maternal effects or other more varied and dynamic forms of natural mortality (e.g., density-dependent adult survival) could be valuable additions to future modeling exercises.

Parameterization

The model was parameterized to generally represent the life history of three different species – Atlantic cod *G. morhua*, Lake whitefish *Coregonus clupeaformis*, and Yellow perch *Perca flavescens* (Table A1). As in Dunlop et al. (2009), the Atlantic cod parameter values were chosen to resemble the species in the northern part of its range. The parameter values for lake whitefish and yellow perch were estimated to resemble Great Lakes populations. The parameter

values chosen resulted in modeled populations that reflected the different life histories characteristic of each species. As such, Atlantic cod in our model were late maturing, had larger sizes at maturation, and had a lower natural mortality rate than the other species; Lake whitefish had intermediate ages and sizes at maturation and natural mortality; yellow perch had younger ages and smaller sizes at maturation and higher natural mortality.

The initial PMRN intercept, the PMRN width, and the maximum somatic growth rate for each species were chosen so as to produce ages and sizes at maturation, and sizes-at-age that fell within observed ranges (Wang et al. 2008, Dunlop et al. 2009, Doll and Lauer 2013). For simplicity, the slope of the PMRN was set to 0 initially, meaning that the PMRN was horizontal in the initial simulation year but was then free to evolve. To avoid having offspring variance = 0 for the slope, we set the slope at 0.01 in the variance calculations (although the mean initial trait value was still 0). Reproductive investment was calculated by taking observed gonado-somatic index (GSI) values for each species and multiplying by 1.73 to account for the higher energy content of gonad tissue relative to soma (Lester et al. 2004). The GSI was based on Kjesbu et al. (1998) for cod, Johnston et al. (2012) for whitefish, and Heyer et al. (2001) for perch. The fecundity-length relationship was based on Kjesbu et al. (1998) for cod, Kratzer et al. (2007) for whitefish, and Lauer et al. (2005) for yellow perch. The Beverton-Holt stock recruitment constants were chosen to produce a simulated population size (prior to fishing) of about 20,000 individuals.

Data on natural mortality is sparse and uncertain. Our approach was to set natural mortality rates so that cod had the lowest natural mortality, followed by whitefish with an intermediate natural

mortality, and yellow perch with the highest natural mortality. The values chosen were consistent with values used previously and with the estimates that do exist (Gunderson 1997, Ebener et al. 2010). A cost of reproduction was applied that was highest in cod (Kuparinen et al. 2012), low for whitefish, and absent for yellow perch. Higher costs of reproduction in whitefish and perch were not possible because the life histories evolved to unrealistic values for these species. The minimum size limit was set to fall just below the size at maturation for each species, meaning that both immature and mature fish were harvested (size limit was set at 75% of the mean initial PMRN intercept).

More extensive sensitivity analyses of parameters are presented in Dunlop et al. (2007, 2009).

Results of the Eco-Evolutionary Model

The amount of evolution of the PMRN depends on the harvest probability and coefficient of genetic variance CV_G . Harvesting a population with genetic variance leads to a reduction in the PMRN intercept, but little evolution of the PMRN slope: the result is a downward shift of the PMRN, which causes a reduced length at 50% maturation probability for all ages (Figs. A1–A3). A harvest rate of 50% causes more evolution of the PMRN than a harvest rate of 20% (Figs. A1–A3). After 100 years of a harvest moratorium, there is little evidence of reversal towards pre-fishing values (Figs. A1–A3). These basic results are the same as those reported in previous eco-evolutionary models (Dunlop et al. 2007, 2009).

For a given harvest probability, increasing the CV_G results in a downward shift of the PMRN (Figs. A1–A3), and therefore maturation at younger ages (Fig. A4). The joint eco-evolutionary

dynamics of the harvested populations results in changes to the total fecundity, proportion of mature fish, and spawning stock biomass (Fig. A4). When following along for a given harvest rate, increasing evolvability results in maturation at a younger age, a higher proportion of mature fish in the population, a higher reproductive output, and increased spawning stock biomass (Fig. A4). The combined result of these effects, lead to the observed changes in r described in the main text.

During harvesting, the rate of PMRN evolution was fastest for cod, intermediate for whitefish, and slowest for perch (Figs. A1–A3, A5). The rate of evolutionary recovery in a subsequent moratorium was much slower than the initial rate of evolution during fishing (Fig. A5). The rate of extinction was lower when genetic variation was higher, and was the highest for perch (Fig. A6). Increasing the strength of density-dependent growth resulted in slightly less PMRN evolution during fishing, but then a slightly higher rate of PMRN recovery during a moratorium (Fig. A5). Increasing the strength of density-dependent growth (by increasing α) also resulted in an overall increase in the difference for r between an evolutionary and non-evolutionary model (Fig. A7).

LITERATURE CITED

- Doll, J. C., and T. E. Lauer. 2013. Bayesian estimation of age and length at 50% maturity. *Transactions of the American Fisheries Society* 142:1012–1024.
- Dunlop, E. S., M. Heino, and U. Dieckmann. 2009. Eco-genetic modeling of contemporary life-history evolution. *Ecological Applications* 19:1815–1834.
- Dunlop, E. S., B. J. Shuter, and U. Dieckmann. 2007. Demographic and evolutionary consequences of selective mortality: Predictions from an eco-genetic model for smallmouth bass. *Transactions of the American Fisheries Society* 136:749–765.
- Ebener, M. P., T. O. Brenden, and M. L. Jones. 2010. Estimates of fishing and natural mortality rates for four lake whitefish stocks in Northern Lakes Huron and Michigan. *Journal of Great Lakes Research* 36:110–120.
- Falconer, D. S., and T. F. C. Mackay. 1996. *Introduction to Quantitative Genetics*. Fourth edition. Longman, Essex, U.K.
- Gunderson, D. R. 1997. Trade-off between reproductive effort and adult survival in oviparous and viviparous fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 54:990–998.
- Heino, M., U. Dieckmann, and O. R. Godø. 2002. Measuring probabilistic reaction norms for age and size at maturation. *Evolution* 56:669–678.
- Heyer, C. J., T. J. Miller, F. P. Binkowski, E. M. Caldarone, and J. A. Rice. 2001. Maternal effects as a recruitment mechanism in Lake Michigan yellow perch (*Perca flavescens*). *Canadian Journal of Fisheries and Aquatic Sciences* 58:1477–1487.
- Hilborn, R., and C. J. Walters. 1992. *Quantitative fisheries Stock Assessment: Choice, Dynamics and Uncertainty*. Chapman & Hall, New York, NY, U.S.A.

- Johnston, T. A., D. M. M. Wong, M. D. Moles, M. D. Wiegand, J. M. Casselman, and W. C. Leggett. 2012. Reproductive allocation in exploited lake whitefish (*Coregonus clupeaformis*) and walleye (*Sander vitreus*) populations. *Fisheries Research* 125:225–234.
- Jørgensen, C., K. Enberg, E. S. Dunlop, R. Arlinghaus, D. S. Boukal, K. Brander, B. Ernande, A. Gårdmark, F. Johnston, S. Matsumura, H. Pardoe, K. Raab, A. Silva, A. Vainikka, U. Dieckmann, M. Heino, and A. D. Rijnsdorp. 2007. Managing evolving fish stocks. *Science* 318:1247–1248.
- Kjesbu, O. S., P. R. Witthames, P. Solemdal, and M. G. Walker. 1998. Temporal variations in the fecundity of Arcto-Norwegian cod (*Gadus morhua*) in response to natural changes in food and temperature. *Journal of Sea Research* 40:303–321.
- Kratzer, J. F., W. W. Taylor, and M. Turner. 2007. Changes in fecundity and egg lipid content of lake whitefish (*Coregonus clupeaformis*) in the upper Laurentian Great Lakes between 1986-87 and 2003-05. *Journal of Great Lakes Research* 33:922–929.
- Krebs, C. J. 1994. *Ecology*. Harper Collins College Publishers, New York.
- Kuparinen, A., D. C. Hardie, and J. A. Hutchings. 2012. Evolutionary and ecological feedbacks of the survival cost of reproduction. *Evolutionary Applications* 5:245–255.
- Kuparinen, A., and J. A. Hutchings. 2012. Consequences of fisheries-induced evolution for population productivity and recovery potential. *Proceedings of the Royal Society B-Biological Sciences* 279:2571–2579.
- Lauer, T. E., S. M. Shroyer, J. M. Kilpatrick, T. S. McComish, and P. J. Allen. 2005. Yellow perch length-fecundity and length-egg size relationships in Indiana waters of Lake Michigan. *North American Journal of Fisheries Management* 25:791–796.

- Lester, N. P., B. J. Shuter, and P. A. Abrams. 2004. Interpreting the von Bertalanffy model of somatic growth in fish: the cost of reproduction. *Proceedings of the Royal Society of London Series B* 271:1625–1631.
- Reznick, D. N. 1993. Norms of reaction in fishes. Pages 72–90 *in* T. K. Stokes, J. M. McGlade, and R. Law, editors. *The exploitation of evolving resources*. Springer-Verlag, Berlin.
- Wang, H. Y., T. O. Höök, M. P. Ebener, L. C. Mohr, and P. J. Schneeberger. 2008. Spatial and temporal variation of maturation schedules of lake whitefish (*Coregonus clupeaformis*) in the Great Lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 65:2157–2169.

TABLE A1. Parameter values for the individual-based eco-evolutionary model. Evolving traits in this model are the slope and intercept of a probabilistic maturation reaction norm (PMRN).

Description	Symbol	Atlantic cod	Lake whitefish	Yellow perch
Initial mean genetic PMRN intercept (cm)*	\bar{l}_G	80	48	18
Initial mean genetic PMRN slope (cm yr ⁻¹)*	\bar{s}_G	0	0	0
Initial heritability*	h^2	0.2	0.2	0.2
Initial standard deviation of growth rate (cm)*	g_{sd}	1.5	1.2	0.6
Initial genetic coefficient of variation* [‡]	CV_G	0-12% in steps of 1%	0-12% in steps of 1%	0-12% in steps of 1%
Starting population size*	N_0	10,000	10,000	10,000
Reproductive investment	R	0.2	0.43	0.72
Maximum annual somatic growth increment (cm)	β	15	12	6
Length-weight allometric constant (g cm ^{-γ})	ν	0.01	0.01	0.01
Length-weight allometric exponent	γ	3	3	3
Fecundity-length exponent	b	3.4526	2.99	3.223
Fecundity-length constant (g cm ^{-γ})	ε	0.00000361	0.000182	0.00060256
Beverton-Holt	δ	$1.0 \cdot 10^{-5}$	$2.5 \cdot 10^{-5}$	$2.5 \cdot 10^{-5}$

constant 1				
Beverton-Holt constant 2	μ	$2.6 \cdot 10^{-9}$	$2.0 \cdot 10^{-9}$	$1.0 \cdot 10^{-9}$
Growth-biomass constant (g^{-1}) [‡]	α	$1.02 \cdot 10^{-8}$ or 1.52×10^{-7}	$1.02 \cdot 10^{-8}$ or 1.52×10^{-7}	$1.02 \cdot 10^{-8}$ or 1.52×10^{-7}
Growth-biomass exponent	δ	0.3	0.3	0.3
PMRN width (cm)	W	40	20	18
Immature natural mortality probability	m_i	0.12	0.37	0.5
Mature natural mortality probability	m_m	0.2	0.39	0.5
Minimum size limit of fishery (cm)	L_H	60	36	13.5
Harvest mortality rate (%) [‡]	F	0-100 in steps of 10	0-100 in steps of 10	0-100 in steps of 10

* Initial parameters which are then free to change after the first simulation year.

[‡] Parameter was manipulated to observe effects on model results.

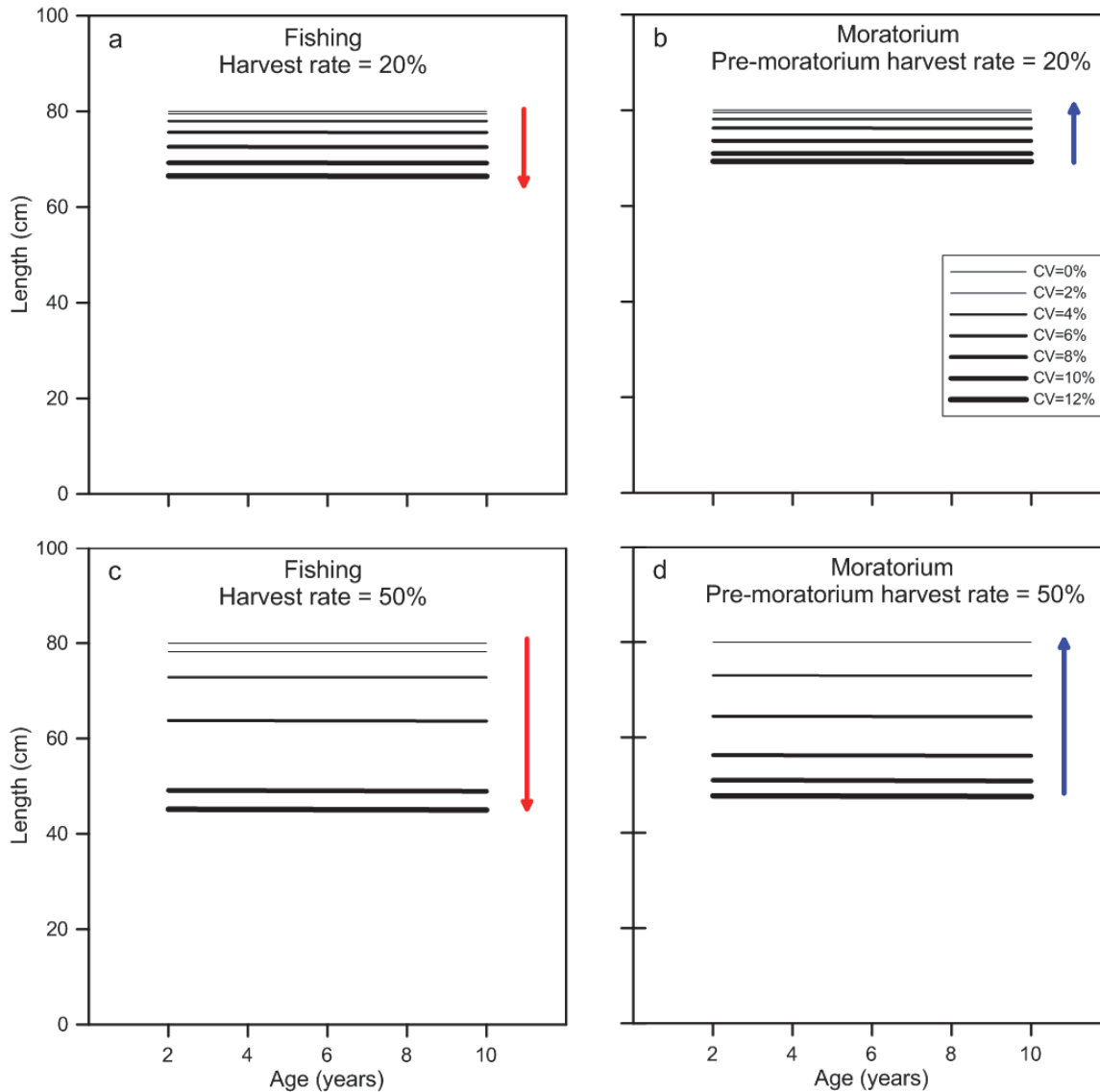


FIG. A1. Evolution of the probabilistic maturation reaction norm (PMRN) for Atlantic cod. Horizontal lines are the midpoints of the PMRN, which represent the length at 50% maturation probability for a given age. Results for two different harvest rates (20% and 50%) are shown. The coefficient of genetic variation (CV_G ; a measure of evolvability), was manipulated. Panels **a** and **c** show the PMRN midpoints after 100 years of fishing at a harvest rate of either 20% or 50%. Panels **b** and **d** show the PMRN midpoints after 100 years of a harvest moratorium (implemented after 100 years of fishing at a given harvest rate). The blue arrow shows the direction of evolution with fishing and the red arrows show the return trajectory of the PMRN during a moratorium. Results are averaged over 10 independent simulation runs.

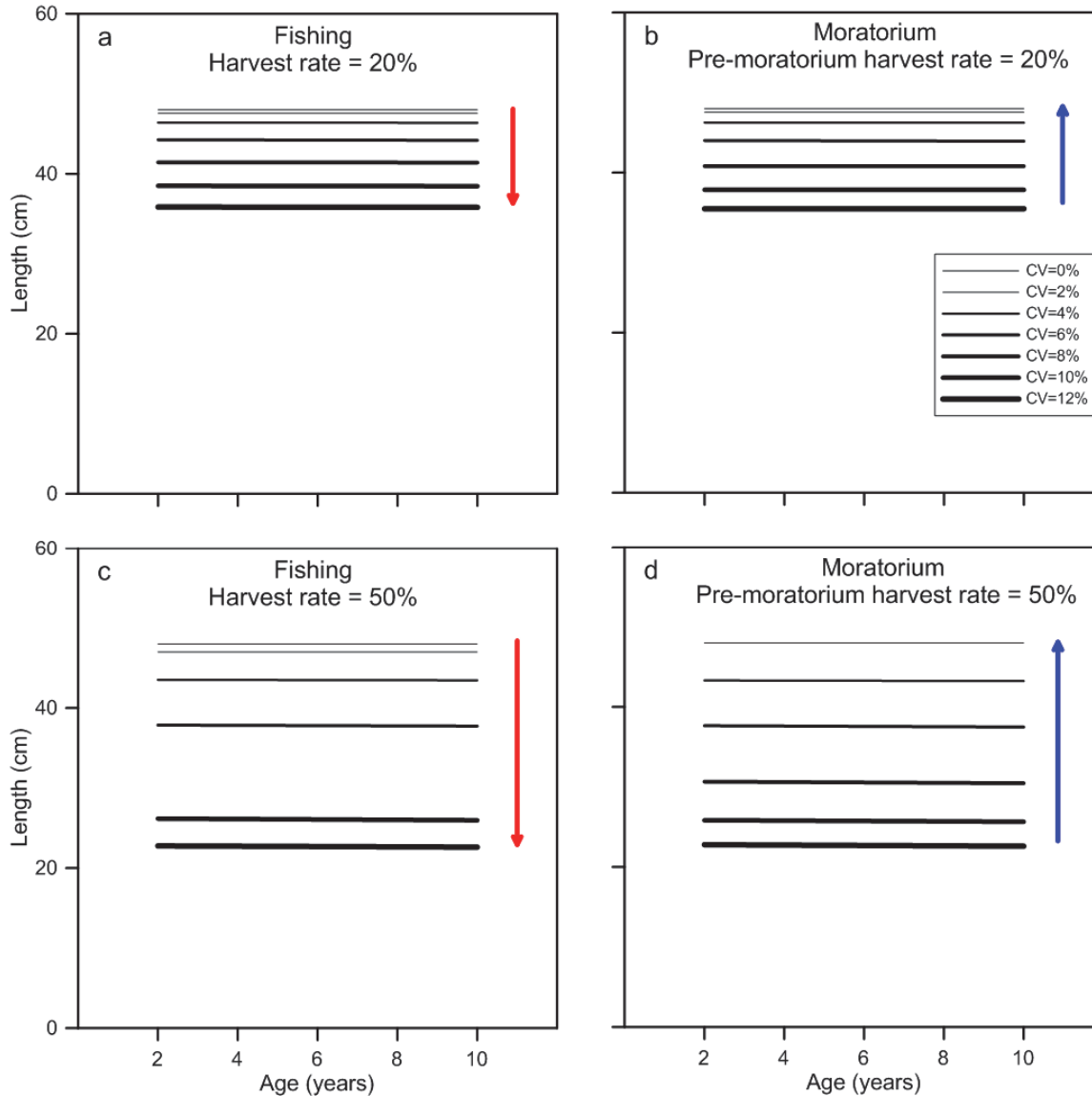


FIG. A2. Evolution of the probabilistic maturation reaction norm (PMRN) for lake whitefish. Horizontal lines are the midpoints of the PMRN, which represent the length at 50% maturation probability for a given age. Results for two different harvest rates (20% and 50%) are shown. The coefficient of genetic variation (CV_G ; a measure of evolvability), was manipulated. Panels **a** and **c** show the PMRN midpoints after 100 years of fishing at a harvest rate of either 20% or 50%. Panels **b** and **d** show the PMRN midpoints after 100 years of a moratorium (implemented after 100 years of fishing at a given harvest rate). The blue arrow shows the direction of evolution with fishing and the red arrows show the return trajectory of the PMRN during a moratorium. Results are averaged over 10 independent simulation runs.

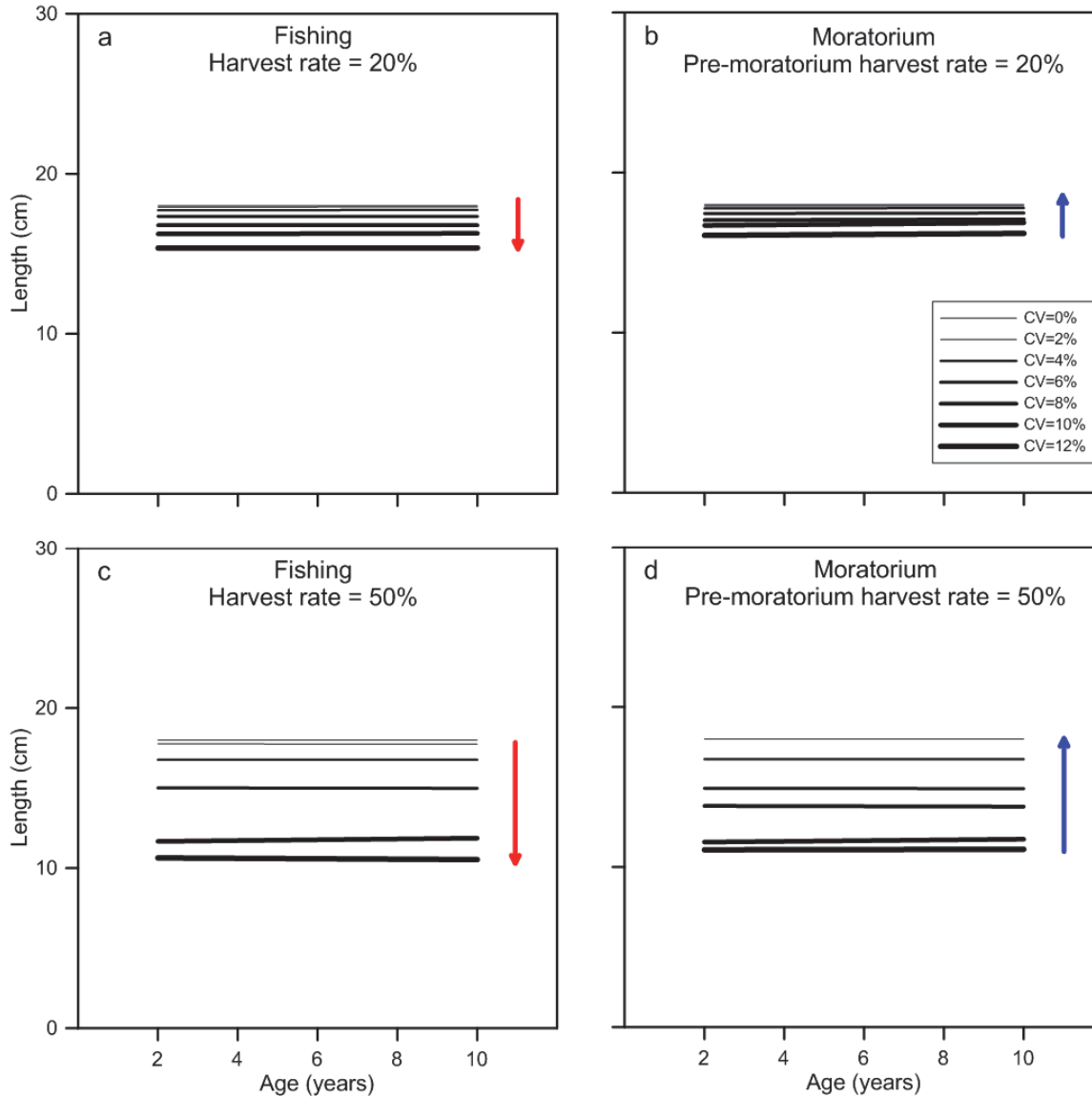


FIG. A3. Evolution of the probabilistic maturation reaction norm (PMRN) for yellow perch. Horizontal lines are the midpoints of the PMRN, which represent the length at 50% maturation probability for a given age. Results for two different harvest rates (20% and 50%) are shown. The coefficient of genetic variation (CV_G ; a measure of evolvability), was manipulated. Panels **a** and **c** show the PMRN midpoints after 100 years of fishing at a harvest rate of either 20% or 50%. Panels **b** and **d** show the PMRN midpoints after 100 years of a moratorium (implemented after 100 years of fishing at a given harvest rate). The blue arrow shows the direction of evolution with fishing and the red arrows show the return trajectory of the PMRN during a moratorium. Results are averaged over 10 independent simulation runs.

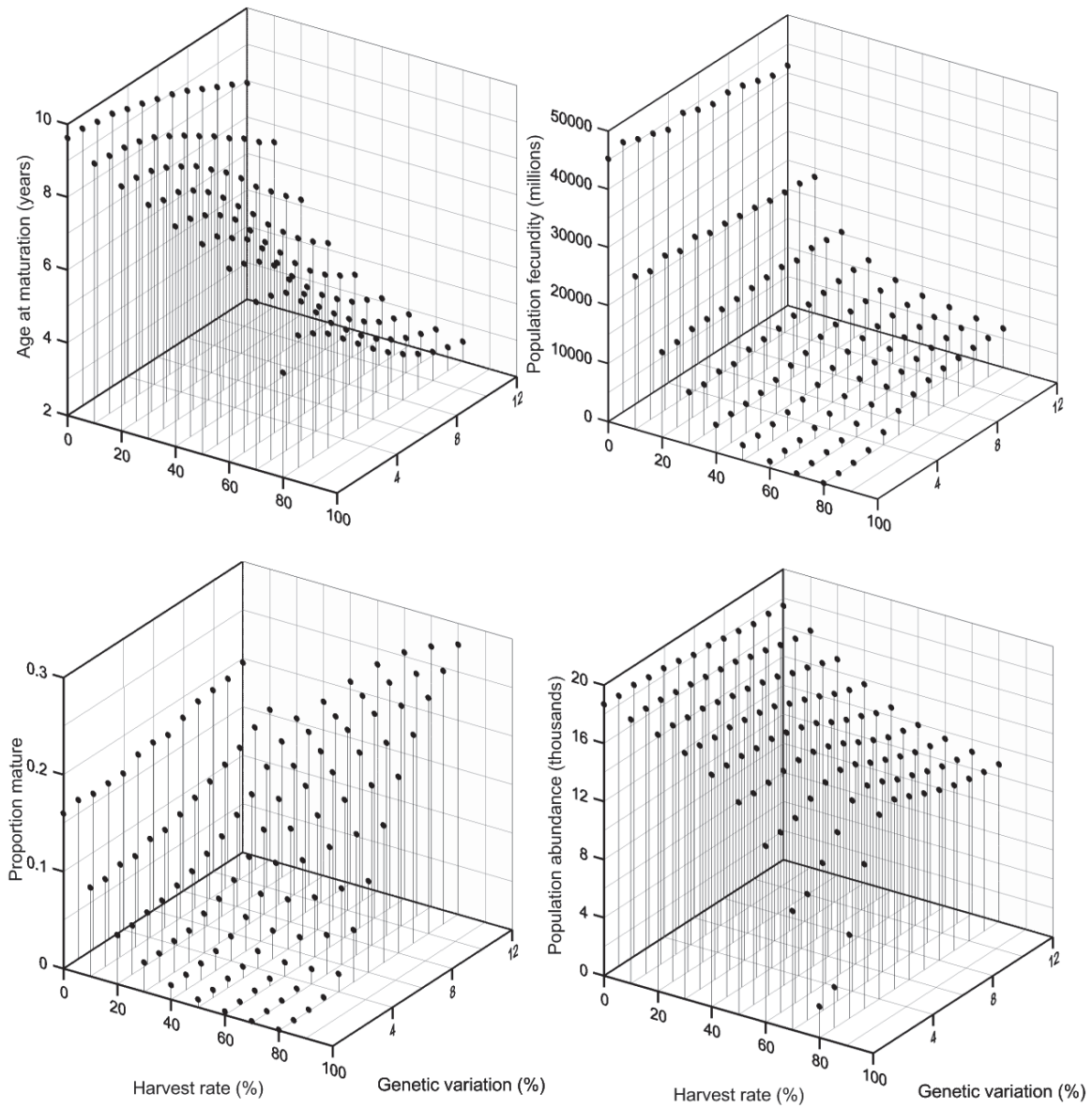


FIG. A4. The response to harvest in key population attributes of Atlantic cod. Results are shown after 100 years of harvesting at a given harvest rate and coefficient of genetic variation. Results are averaged over 10 independent simulation runs.

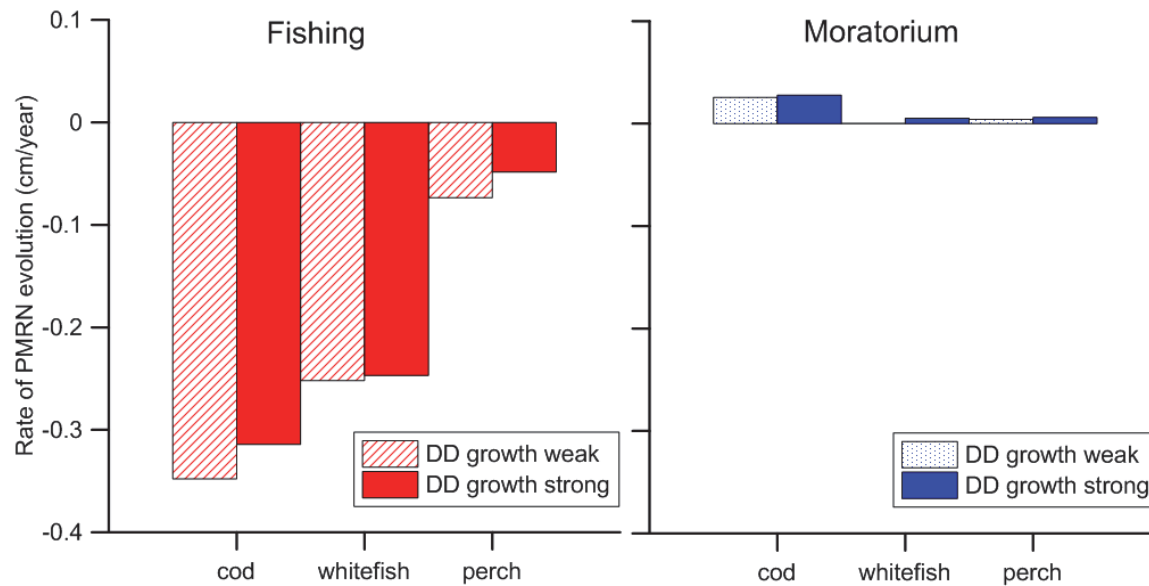


FIG. A5. The effects of varying the strength of density-dependent growth on the rate of probabilistic maturation reaction norm (PMRN) evolution. The fishing panel shows the rate during 100 years of fishing at a harvest rate of 50% and a coefficient of genetic variation of 12%. The right panel shows the rate of PMRN evolution during a subsequent harvest moratorium, also applied for 100 years. Negative values during fishing indicate a downward shift of the PMRN, whereas positive values during a moratorium indicate an upward shift of the PMRN from the year when the moratorium began. Results are averaged over 10 independent simulation runs.

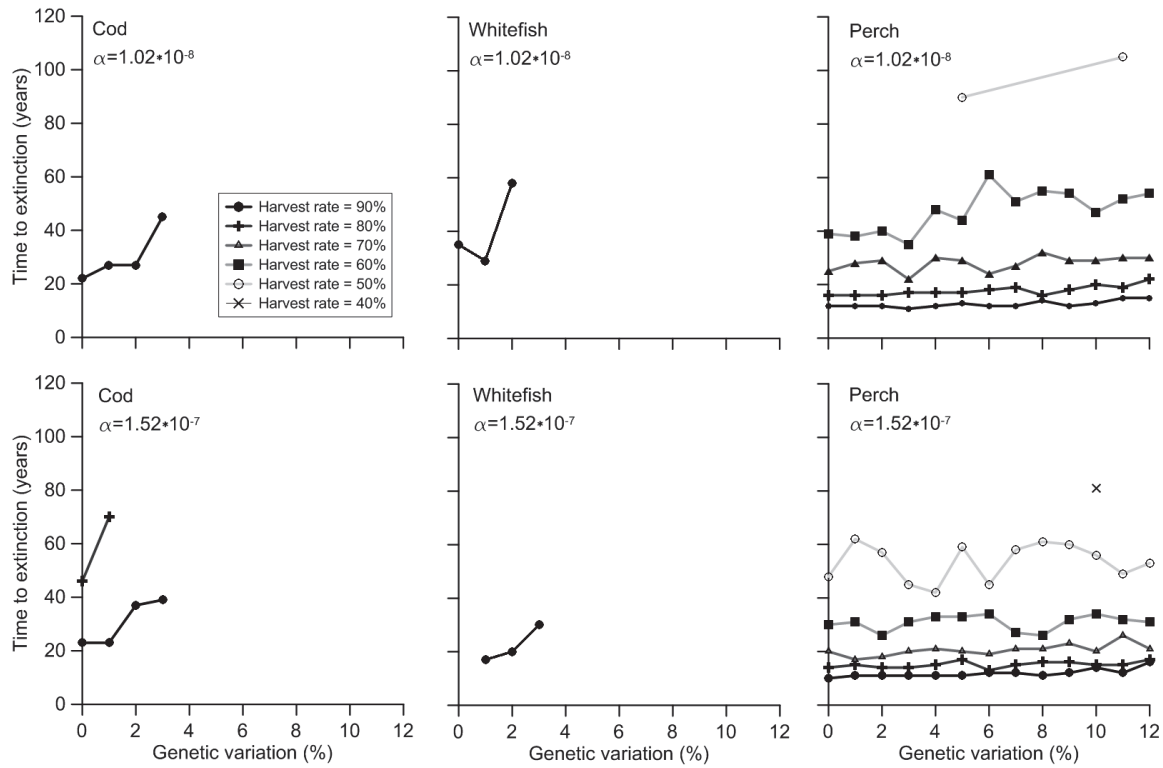


FIG. A6. The effects of varying the strength of density-dependent growth on the time to population extinction. Simulations where the population did not go extinct are not shown. Top panels are the baseline values for the density-dependent growth parameter α used in the main text. Bottom panels show the results where density-dependent growth compensation was strengthened by increasing α .

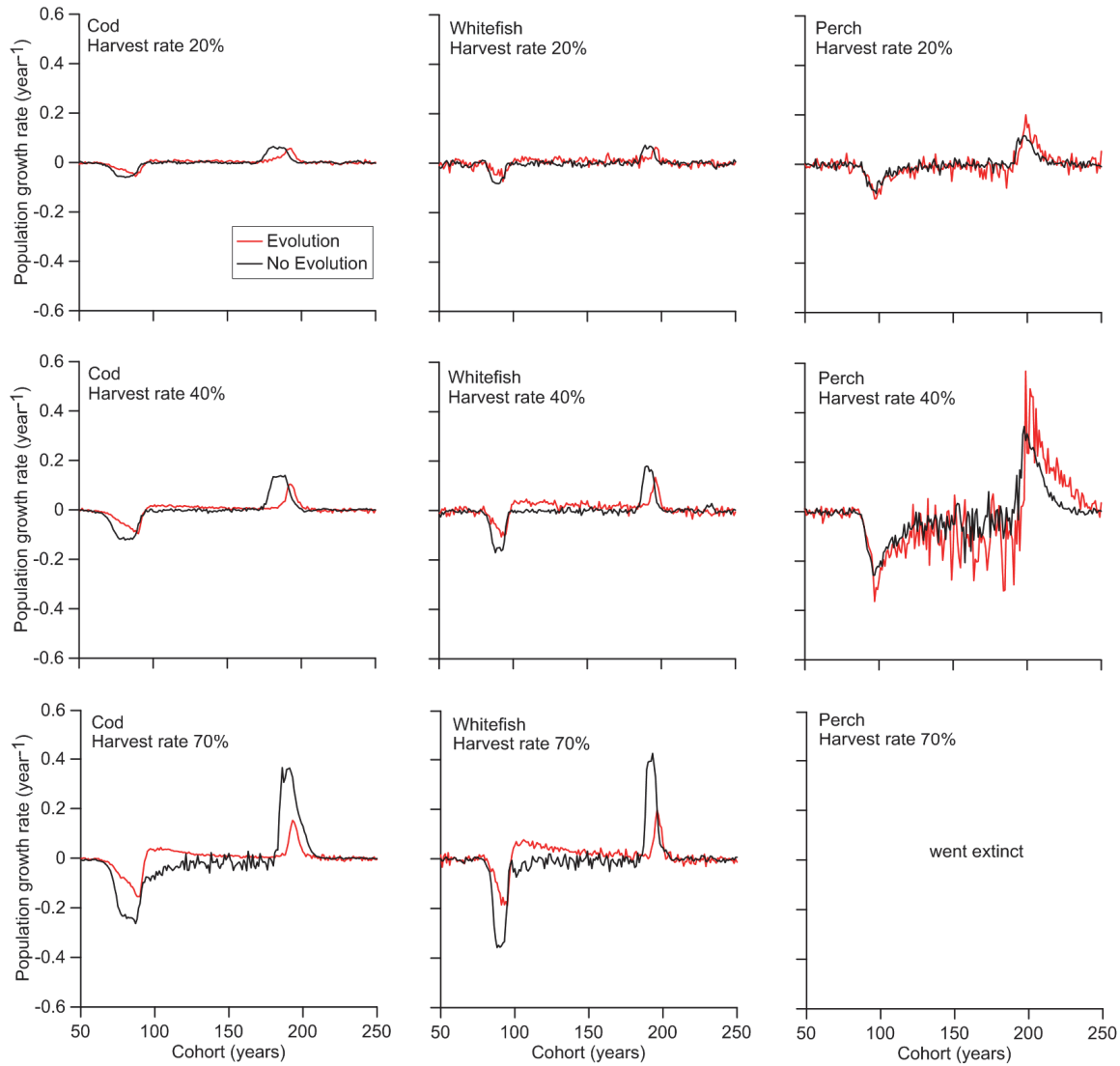


FIG. A7. Trends in population growth rate r for three example harvest rates (20, 40, and 70%). The parameter α in the density-dependent growth relationship was increased to 1.52×10^{-7} relative to the baseline scenarios (Fig. 3) where α was 1.02×10^{-8} . The coefficient of genetic variance CV_G was 12% in this evolutionary scenario. Harvest was initiated in year 100 and a harvest moratorium was implemented in year 200. Results are averaged over 10 independent simulation runs. Note that the x axis is cohort, and not simulation year, and therefore the effects of fishing or a moratorium are first experienced by the older individuals that were born in previous years.