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Eco-genetic modelling of contemporary life-history evolution

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Contents

Eco-genetic Modeling of Contemporary Life-History Evolution

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Abstract.   We present eco-genetic modeling as a flexible tool for exploring the course and rates of multi-trait life-history evolution in natural populations. We build on existing modeling approaches by combining features that facilitate studying the ecological and evolutionary dynamics of realistically structured populations. In particular, the joint consideration of age and size structure enables the analysis of phenotypically plastic populations with more than a single growth trajectory, and ecological feedback is readily included in the form of density dependence and frequency dependence. Stochasticity and life-history trade-offs can also be implemented. Critically, eco-genetic models permit the incorporation of salient genetic detail such as a population's genetic variances and covariances, the corresponding heritabilities, as well as the probabilistic inheritance and phenotypic expression of quantitative traits. These inclusions are crucial for predicting rates of evolutionary change on both contemporary and longer timescales. An eco-genetic model can be tightly coupled with empirical data and therefore may have considerable practical relevance, in terms of generating testable predictions and evaluating alternative management measures. To illustrate the utility of these models, we present as an example an eco-genetic model used to study harvest-induced evolution of multiple traits in Atlantic cod. The predictions of our model – most notably that harvesting induces a genetic reduction in age and size at maturation, an increase or decrease in growth capacity depending on the minimum size limit, and an increase in reproductive investment – are corroborated by patterns observed in wild populations. The predicted genetic changes occur together with plastic changes that could phenotypically mask the former. Importantly, our analysis predicts that evolutionary changes show little signs of reversal following a harvest moratorium. This illustrates how predictions offered by eco-genetic models can enable and guide evolutionarily sustainable resource management.
Key words: life-history theory; phenotypic plasticity; density-dependent growth; evolution; fishing-induced adaptive change; fisheries-induced evolution; harvest; reproductive

investment; probabilistic maturation reaction norm; quantitative genetics; eco-evolutionary

dynamics

Introduction

Throughout the natural world, tremendous diversity exists in the life histories of

organisms. The central goal of evolutionary ecology is to understand the processes that create

and maintain this diversity (Roff 1992, Stearns 1992). Such a goal is an important and worthy

endeavor because the life-history characteristics of organisms influence biodiversity patterns,

dictate the response of populations to anthropogenic environmental change, shape the

exploitation patterns of humans, and play a crucial role in the success of invading exotic

species. Models are indispensable tools in all of these areas because they provide a basis for

understanding the often intricate mechanisms involved in creating and altering life-history

variation, and can be used to guide empirical work. Models can, and should, also be used

proactively to predict the effects of human activities (such as harvest, pollution, or habitat

alteration) on organisms and their life-history characteristics. In this article we describe a tool,

eco-genetic modeling, that is based on building blocks that are mostly well established, but are

here combined in a novel way. Eco-genetic models are designed to study life-history evolution

on contemporary timescales and to establish a tight coupling with empirical data, thus

improving the practical relevance offered by many previous models.

Several approaches have been devised for examining the evolution of life-history traits.

Commonly employed theoretical tools include optimization models, quantitative genetics

models, and adaptive dynamics models. Optimization models (e.g., Cole 1954, Maynard

Smith 1978, Law 1979, Orzack and Sober 1994, Day and Rowe 2002) are the most traditional

and widely used type of life-history model (Mangel and Clark 1989, Roff 1992, Stearns 1992).

In an optimization model, a chosen measure of fitness is maximized – usually either lifetime

reproductive output or a population's rate of increase. Optimization models can only predict evolutionary endpoints under frequency-independent selection, which correspond to maxima of a chosen fitness measure. In a traditional optimization model, the life-history traits in question are represented as phenotypes and there is no consideration of underlying genetic detail (Bull et al. 2004). Quantitative genetics models (e.g., Gomulkiewicz and Kirkpatrick 1992, Kirkpatrick 1993, Van Tienderen 1997, Baskett et al. 2005) differ from optimization models by including such genetic detail. A typical quantitative genetics model will permit a more detailed perspective on genetic mechanisms underlying life-history variation and, thereby, will allow predicting evolutionary rates over a few generations. However, owing to the inevitable evolution of genetic variances and covariances, such models can usually not yield reliable predictions over longer timescales. In adaptive dynamics models (e.g., Dieckmann and Law 1996, Geritz et al. 1998, Nowak and Sigmund 2004), genetic detail is sacrificed in favor of ecological detail, and evolution is modeled as a successive process of invasions by variant phenotypes. The power of adaptive dynamics models results from the fact that in these models, unlike in optimization models and in typical quantitative genetics models, selection can be density-dependent as well as frequency-dependent. This is an advantage because, in the course of evolution, the fitness landscape on which individuals evolve must be expected to change as their environment and, in particular, the phenotypic composition of their conspecifics changes. Selection in such settings is usually both density-dependent and frequency-dependent because the fitness of an individual is a function of its phenotype and environment, with the latter being affected by the type, density, and frequency of other phenotypes in the population (Metz et al. 1992, Heino et al. 1998). Accounting for the complexities of frequency-dependent selection often rules out incorporation of genetic complexity, so that a typical adaptive dynamics model predicts evolutionary endpoints and the shape of evolutionary transients, but is not meant to forecast evolutionary rates in real time, as these rates not only depend on selection pressures but also on a population's genetic variance.

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While these evolutionary modeling approaches have provided the basis of most of our current understanding of life-history theory, they involve a number of simplifications. First, most previous models (e.g., Law and Grey 1989, Getz and Kaitala 1993, Ernande et al. 2004, Tenhumberg et al. 2004, Baskett et al. 2005) do not include density-dependent growth, even though its importance for shaping life-history characteristics and population dynamics has been well documented (Ray and Hastings 1996, Lorenzen and Enberg 2002). Another simplification has been the omission of phenotypic plasticity from many life-history models, even though it controls the phenotypic expression of genetically-based traits by forming a link with the environment (for introductory treatments of phenotypic plasticity see Scheiner 1993, Pigliucci 2005). A third simplification has been the lack of genetic detail: previous models, most notably adaptive dynamics and optimization models, have examined phenotypic evolution without including such information. Predicting rates of evolutionary change in real time is then not possible, which limits thorough comparisons between observed trends and model predictions.

Comprehensive modeling tools are needed if we wish to study the rates of multi-trait evolution while including features such as genetic detail and ecological feedback. Here, we present eco-genetic modeling as an integrative tool for including salient genetic detail in conjunction with important aspects of the ecological setting. The genetic component of an eco-genetic model follows the evolution of the distribution of quantitative traits that are inherited by offspring from their parents. The ecological setting of an eco-genetic model accounts for aspects of an individual's environment that are pertinent to the evolutionary process, including structured population dynamics, phenotypic plasticity, environmental stochasticity, and ecological feedback through density-dependent and frequency-dependent processes. As far as we are aware, eco-genetic modeling is the only tool that simultaneously enables, in the context of realistically structured population dynamics, (i) analyses of density-dependent and frequency-dependent ecological feedback, (ii) predictions of evolutionary rates, transients, and

endpoints, and (iii) incorporation of genetic detail such as mode of inheritance, distribution of genetic variance, and phenotypic expression of quantitative genetic traits. An application of this modeling tool was presented by Dunlop et al. (2007), who used an eco-genetic model to predict the consequences of mortality-induced evolution in introduced populations of smallmouth bass *Micropterus dolomieu*. Another recent application is the eco-genetic model of brook charr *Salvelinus fontinalis* designed to study fishing-induced evolution of anadromous migration and residency (Thériault et al. 2008).

Below, we describe eco-genetic modeling in general and demonstrate its utility for studying life-history evolution. Specifically, we outline the unifying concepts and building blocks underlying these models. By examining harvest-induced evolution, we then highlight a particularly promising application of eco-genetic models. This example is designed to address two questions. First, what are the predicted contemporary consequences of harvesting for the joint evolution of multiple life-history traits? Second, how fast do multiple traits recover following a harvest moratorium? By addressing these questions, we hope to illustrate how eco-genetic models can help us understand complexities of adaptation and predict anthropogenic impacts on natural resources.

An Overview of Eco-genetic Modeling

As the name implies, the goal of eco-genetic modeling is to provide a comprehensive methodology for modeling life-history evolution by including salient genetic detail in conjunction with critical ecological detail (Figure 1). The ensuing eco-genetic dynamics describe how the distribution of genetic traits (not just of their means and variances) changes in the course of Darwinian evolution, as trait values promoting survival and offspring production are demographically favored. Therefore, unlike many traditional life-history models, eco-genetic models do not assume any fitness functions a priori, but, instead, as in adaptive

dynamics models, allow fitness to emerge naturally as a consequence of the underlying population dynamics. It also follows that eco-genetic models allow examining the pathway of evolution, rather than only focusing on evolutionary endpoints, while many traditional life-history models only permit the latter.

Although substantially flexible, eco-genetic models are unified by several key concepts (Figure 1). Below, we briefly outline these concepts and explain why their inclusion is often important for models of life-history evolution.

Process-based description of demographic mechanisms

Eco-genetic models are designed so that population-level and system-level properties emerge from the underlying and realistically modeled individual-level processes of growth, maturation, reproduction, and mortality. Modeling processes in this way allows for a mechanistic approach to demographic change, in lieu of simply providing a phenomenological description of population properties. This process-based approach also means that eco-genetic models can be closely linked with, compared to, and parameterized based on empirical data.

Population structure

Differential survival and reproductive success of individuals in a population will usually depend on aspects such as their age, size, maturation status, condition, sex, and phenotype. Incorporation of the resultant population structure is therefore necessary if we are to predict directions, rates, and magnitudes of life-history evolution with any satisfactory degree of realism and accuracy (e.g., Metz and Diekmann 1986).

Density dependence and frequency dependence

The traditional approach to modeling animal populations in general, and fish populations in particular, is to assume that density dependence acts only during early life stages. When this assumption is made, optimization models can often be used to model life-history evolution. However, it is increasingly being recognized that density dependence also acts during other phases and in conjunction with other aspects of an organism's life cycle. For

example, density-dependent growth must be expected to occur at many stages because the presence of conspecifics alters food availability (Bromley 1989, Rijnsdorp and Van Leeuwen 1992, Ray and Hastings 1996, Post et al. 1999, Lorenzen and Enberg 2002, Persson and de Roos 2006). While it is evident that there are fitness implications of altered growth conditions for body size and thus for survival, maturation, and reproduction, the resultant evolutionary consequences are often intricate (e.g., Ylikarjula et al. 1999, Claessen and Dieckmann 2002, Ylikarjula et al. 2002). Also, an overlap between the density-dependent and trait-dependent portions of an organism's life cycle implies frequency-dependent selection. This precludes the application of optimization models and of quantitative genetics models based on frequency-independent selection, thus requiring another approach such as the one we are proposing here. Furthermore, harvest by humans, like any other type of predation, can be density-dependent (Hilborn and Walters 1992). Comprehensive eco-genetic models must therefore consider the importance of population abundances, densities, and biomasses for shaping demographic and evolutionary processes.

Phenotypic plasticity

Many life-history traits exhibit phenotypic plasticity (Stearns 1989, Pigliucci 2005), such as when ambient temperature affects growth or when fast-growing individuals tend to mature younger. As selection acts on the phenotypes of individuals, phenotypic plasticity can influence the rates and endpoints of evolution, especially in temporally or spatially heterogeneous environments (e.g., Ernande et al. 2004). For example, in the quantitative genetics model of Baskett et al. (2005), including phenotypic plasticity in size at maturation produced rates of fisheries-induced evolution in Atlantic cod (*Gadus morhua*) that more closely matched empirical trends than when plasticity was not considered.

Stochasticity

The sources of stochastic variation potentially relevant in eco-genetic models span from genetic processes and the micro-environment of an individual to inter-annual variation in the

macro-environment experienced by a population. Stochasticity can be incorporated in an eco-genetic model so that the genotypes, phenotypes, events, demographic rates, or environment are affected, without a need for explicit modeling of the detailed mechanisms underlying such variability (e.g., Grimm and Railsback 2005). Temporal autocorrelation of stochastic noise can also be incorporated, for example, if there is an interest in modeling time series of temperature effects (Steele 1985, Halley 1996). Stochasticity is particularly important for the evolution of bet-hedging strategies such as dormancy, iteroparity, and dispersal (e.g., Murphy 1968, Levin et al. 1984, Venable and Brown 1988).

Genetic variation

Evolving traits in an eco-genetic model genetically vary between individuals, with a component of their phenotypic variation being heritable. With heritable variability being a prerequisite for adaptive evolutionary change, genetic variance has a strong influence on the speed of such processes (Houle 1992, Dunlop et al. 2007). In response to strong selection pressures, such as those resulting from severe anthropogenic environmental impacts, the distribution of genetic variation can deviate substantially from being normal, thus defying simplified descriptions merely based on means and variances. Furthermore, for purposes of comparison and understanding, it is often illuminating to switch off evolution in eco-genetic models by making populations genetically monomorphic or by making variability non-heritable.

Trade-offs

Life-history traits are typically traded off against one another, so that an increase in one component of fitness will cause a decrease in another (Stearns 1992). A ubiquitous trade-off to be captured in an eco-genetic model is that between somatic growth and reproductive investment. Other trade-offs might occur between growth and survival or between reproductive investment and survival. These trade-offs are common in nature and lie at the heart of life-history theory because they crucially shape the life-history strategies, energy

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allocation patterns, and behaviors of individuals (Law 1979, Roff 1992, Stearns 1992, Gunderson 1997, Lester et al. 2004).

Building Blocks of Eco-genetic Models

There are a number of basic considerations to make when constructing an eco-genetic model. The paragraphs below give a summary of the essentials and, together with Table 1, provide guidelines for building models of this type.

Evolving traits

Perhaps the foremost decision is which evolving trait(s) to include. As a consequence of their design, and to keep analyses simple, most previous life-history models have included only one evolving trait, or seldom, two evolving traits (e.g., Abrams and Rowe 1996, Doebeli and Ruxton 1997, Taborsky et al. 2003, Baskett et al. 2005). It is obvious, however, that the interplay between multiple evolving traits will bring new insights. For example, the evolutionary response in a trait evolving alone could well be larger than the response of that same trait in a model considering simultaneous evolution of other traits. In explorations of life-history evolution, common traits to include are genetic determinants of maturation tendency, growth capacity, and reproductive investment.

When choosing to model multiple traits, genetic covariances between traits can be added explicitly or could emerge from the ensuing ecological and evolutionary dynamics. The matrix of genetic variances and between-trait covariances (the G-matrix) can constrain the pathway of multi-trait evolution and undergo evolutionary change itself (Steppan et al. 2002). For an example of how to include genetic correlations explicitly and how to estimate the G-matrix in an individual-based model, see Jones et al. (2003). Quantifying the covariances will, however, usually present a challenge owing to a lack of empirical data. For simplicity, covariances will thus often not be included in a model's initial conditions, but will instead be

allowed to evolve as emergent properties of an eco-genetic model. Using eco-genetic models

to examine the influence of initial covariances on evolution and how the G-matrix is expected

to evolve in response to realistic selection pressures is an exciting avenue for future research.

Inheritance model

An important feature of eco-genetic models is the inheritance of genetic traits from

parents to offspring. There are two commonly considered, alternative models of inheritance:

allelic and quantitative genetic. In an allelic model, as in classic population genetics (Hartl and

Clark 2007), individual alleles are modeled as being passed on directly from parents to

offspring (e.g., Getz and Kaitala 1993, Tenhumberg et al. 2004); the advantage is that no

assumptions are made about the offspring trait distribution. This choice also permits

specification of haploid versus diploid inheritance of loci and the inclusion of non-additive

effects such as dominance and epistasis. However, a quantitative genetics approach is typically

used in eco-genetic models because most life-history traits are regarded as polygenic

quantitative characters (Roff 1992, Conner and Hartl 2004), which are assumed to be affected

by a large number of genetic loci, each with small effects (Falconer and Mackay 1996, Lynch

and Walsh 1998). In a quantitative genetics model, offspring typically inherit the genetic traits

of their parents from a normal distribution with a mean equal to the mid-parental value (i.e., the

arithmetic mean trait value of the two parents) and a suitably chosen variance-covariance

matrix σ_{SR}^2 reflecting the action of segregation and recombination among the underlying, and

not explicitly modeled, loci (Roughgarden 1979). The effects of mutations on the considered

quantitative traits can be included in this matrix. Denoting the maternal and paternal trait

variance-covariance matrices by σ_M^2 and σ_F^2, respectively, the variance-covariance matrix σ_O^2

of the offspring's trait distribution is $\sigma_O^2 = \frac{1}{4}(\sigma_M^2 + \sigma_F^2) + \sigma_{SR}^2$. The factor $\frac{1}{4}$ arises here

because the sum of the two parental trait values is divided by 2 to obtain the offspring's trait

value; for the offspring variance, this division by 2 implies a division by $2^2 = 4$. When

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parsimoniously assuming that $\sigma_M^2 = \sigma_F^2 = \sigma_{M,F}^2$, where $\sigma_{M,F}^2$ is known as the population's G-

matrix, the offspring's variance-covariance matrix is given by

$$\sigma_O^2 = \tfrac{1}{2}\sigma_{M,F}^2 + \sigma_{SR}^2 \ . \tag{1}$$

After genetic traits are inherited from parents to offspring, they are expressed phenotypically.

The phenotypic variance $\sigma_P^2 = \sigma_G^2 + \sigma_E^2$ of a trait depends on the additive genetic variance σ_G^2

and on the environmental variance σ_E^2. The corresponding heritability h^2 is defined by the

ratio of these genetic and phenotypic variances, $h^2 = \sigma_G^2 / \sigma_P^2$.

Sometimes, it might also be desirable to combine the description of quantitative genetic

life-history traits with an allelic representation of neutral genetic markers. This enables

analysis of genetic relatedness and diversity.

Segregation-recombination variance-covariance

If a quantitative genetics model is used, there are at least three possible options for

modeling the variances and covariances of the trait values of offspring originating from a given

pair of parents (Equation 1). The first option is to assume a constant variance-covariance

matrix σ_{SR}^2 that remains unchanged through time (corresponding to a constant segregation-

recombination kernel; Roughgarden 1979). This assumes that the processes of segregation and

recombination contribute a constant amount of variation even as trait values are evolving. The

second option is to assume that the population's variance-covariance matrix is stable,

$\sigma_O^2 = \sigma_{M,F}^2$, implying $\sigma_{SR}^2 = \tfrac{1}{2}\sigma_{M,F}^2$, so that the segregation-recombination variance-covariance

matrix always equals half the population's G-matrix in the parental generation (e.g., Cavalli-

Sforza and Feldman 1976, Baskett et al. 2005). This option thus assumes that the segregation-

recombination variance-covariance matrix σ_{SR}^2 changes in the course of evolution so as to

exactly compensate any selection-induced changes in a population's G-matrix $\sigma_{M,F}^2$. While

such an assumption is formally convenient, it may be deemed unrealistic – not only because

there is no mechanistic basis for expecting such exact compensation, but also because this option implies that, at one moment in time, the segregation-recombination variances and covariances for all pairs of parents are identical and determined by the current variances and covariances of the entire parental generation. The third option allows variation of the segregation-recombination variances and covariances not only in time but also between pairs of parents. This is achieved in two steps, by assuming that each of the offspring standard deviations $\sigma_{\mathrm{SR}\,ii}$ for traits $i = 1,\ldots,n$ (where i, just as j below, is a trait index and n denotes the total number of traits considered) equals half the difference in the corresponding parental trait values, and by scaling the offspring covariances $\sigma_{\mathrm{SR}\,ij}^2$ proportionally

($\sigma_{\mathrm{SR}\,ij}^2 \sigma_{\mathrm{SR}\,ii}^{-1} \sigma_{\mathrm{SR}\,jj}^{-1} = \sigma_{\mathrm{M,F}\,ij}^2 \sigma_{\mathrm{M,F}\,ii}^{-1} \sigma_{\mathrm{M,F}\,jj}^{-1}$ for $i, j = 1,\ldots,n$). This reflects the intuitive assumption that parents that vary greatly from one another will have offspring that also vary greatly. In addition, it can be shown that the third option ensures the evolutionary invariance of normal distributions under segregation and recombination. The first option above can be used to constrain or direct the evolution of a population's G-matrix, whereas the second and third option can allow the population's G-matrix to evolve more freely as an emergent property of the model.

Growth model

In eco-genetic models, somatic growth can be described using one of many existing growth models that incorporate the important trade-off between allocation to somatic growth and investment in reproduction. One of these models is that of Lester et al. (2004). In this model, length at birth is 0 cm (the model is readily generalized by incorporating this length as an extra parameter), and the somatic growth of immature individuals is linear, with an annual phenotypic length increment g_{D}. For mature individuals, there is a trade-off between somatic growth and reproductive investment,

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$$l_{a+1} = \frac{3}{3 + \gamma GSI_{\mathrm{P}}}(l_a + g_{\mathrm{D}}) \; , \tag{2a}$$

where l_a is body length at age a, GSI_{P} is the phenotypic gonado-somatic index (gonad weight divided by somatic weight), and γ is a conversion factor to account for the higher energy density of gonad tissue relative to somatic tissue (Lester et al. 2004). The above growth model is based on assuming that somatic growth and gonad development occur sequentially during each annual growing season and that the portion of an individual's body weight given by gonads does not contribute to its weight acquisition. Weight at age, w_a, can be calculated from length at age, $w_a = \mu l_a^{\alpha}$, with allometric constants μ and α.

An alternative growth model described by Roff (1983) is analogous to that by Lester et al. (2004), except that Roff (1983) assumed gonad weight to contribute to weight acquisition. This implies that larger gonads facilitate weight acquisition, which is generally unrealistic. Mature individuals in Roff's model grow according to

$$l_{a+1} = \frac{1}{\sqrt[3]{1 + \gamma GSI_{\mathrm{P}}}}(l_a + g_{\mathrm{D}}) \; . \tag{2b}$$

The growth model by West et al. (2001) was introduced based on fundamental physiological principles. In this model, body weight w_a at age a depends on asymptotic body weight w_{∞}, body weight at birth w_0, and on a parameter b,

$$(w_a / w_{\infty})^{1/4} = 1 - [1 - (w_0 / w_{\infty})^{1/4}] \exp(-\tfrac{1}{4} abw_{\infty}^{-1/4}) \; . \tag{2c}$$

This relation might be less convenient for modeling evolution of traits like growth capacity and reproductive investment, because annual length increments and gonado-somatic indices here are an outcome of annual integration, whereas they serve as parameters in the models by Lester et al. (2004) and Roff (1983).

The above models are based on fairly simple bioenergetics. The advantage of using such growth models is that they possess fewer parameters than complex models and that the

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values of their traits are often more readily compared with data. Depending on needs and

interest, the behavior and physiology underlying growth can of course be modeled in more

complex ways. For example, energy acquisition (in terms of willingness to forage and take

risks) and allocation (in terms of internal processes causing investments in growth and

reproduction) can be modeled more explicitly and based on additional evolving traits.

The growth models above capture the ubiquitous trade-off between growth and

reproduction. Less commonly considered, but nonetheless potentially very influential, is the

trade-off between growth and survival. This trade-off applies when fast growth incurs a cost,

for example, because rapidly growing individuals invest less energy into basal metabolism

(Nicieza and Metcalfe 1999, Billerbeck et al. 2001, Carlson et al. 2004) or because fast growth

is enabled by a more risky foraging strategy (Walters and Juanes 1993). Both cases result in

elevated mortality for individuals with a capacity for fast growth. The simplest representation

of this trade-off arises when the resultant annual mortality probability increases linearly with

the genetic growth capacity g_G, from 0 to a maximum of 1,

$$m_g = g_G / g_{max} \ .$$
(2d)

This trade-off can be adjusted in strength by altering the maximal annual growth increment

g_{max}, at which annual survival would drop to 0.

Density dependence

Density dependence can be incorporated into an eco-genetic model in many forms,

acting on newborn mortality, somatic growth, cannibalism, and/or harvesting. For example,

density-dependent mortality of newly born offspring can be described with the help of an

appropriate relation such as the Beverton-Holt model (Beverton and Holt 1957),

$$N_r = \frac{s_0 f_T}{1 + c_1 f_T} \ ,$$
(3a)

or the Ricker model (Ricker 1954),

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$$N_r = s_0 f_T \exp(-c_2 f_T) \ , \tag{3b}$$

where N_r is the number of surviving offspring produced by the population, f_T is the total

fecundity of the mature female population, s_0 is the maximal fraction of offspring that survive,

and c_1 and c_2 are parameters. Notice that the two models above were originally introduced to

describe empirical relationships between spawning stock abundance and recruitment; using

them to represent density-dependent newborn survival allows for a more mechanistic approach.

Generalizations of these stock-recruitment relationships include the Maynard Smith and

Slatkin (1973) model, also known as the Shepherd (1982) model (which displays

overcompensation similar to the Ricker model),

$$N_r = \frac{s_0 f_T}{1 + (c_3 f_T)^{c_4}} \ , \tag{3c}$$

the Hassell (1975) model,

$$N_r = \frac{s_0 f_T}{(1 + c_5 f_T)^{c_6}} \ , \tag{3d}$$

and the Saila-Lorda model (Saila et al. 1988; see also Iles 1994, Needle 2001),

$$N_r = (c_7 f_T)^{c_8} \exp(-c_9 f_T) \ , \tag{3e}$$

with parameters c_3 to c_9. In contrast to the other relationships above, the Saila-Lorda model

can describe depensation, that is, an Allee effect implying reduced offspring survival at low

fecundity. To include such an effect in the other relationships, the term f_T in the numerator of

Equations 3a to 3d can be replaced with $f_T^{c_{10}}$, with $c_{10} > 1$. In lieu of total fecundity f_T,

Equations 3a to 3e could also be based on other fecundity measures such as the total biomass

of the mature population or of the mature female population.

When food and other resources are limiting, a negative relationship between population

biomass and an individual's somatic growth might arise. In this case, the density-dependent

annual phenotypic length increment g_D can be modeled as follows,

$$g_D = \frac{g_P}{1 + (c_{11}B)^{c_{12}}} \quad , \tag{3f}$$

where g_P is the phenotypic growth capacity of an individual, B is population biomass (an emergent property of the model), and c_{11} and c_{12} are parameters. Somatic growth (i.e., growth of the somatic tissue as opposed to growth of gonads) could also be reduced by the biomasses of other species that feed on similar resources.

Other sources of density dependence are cannibalism and harvesting. Survival from cannibalism, $\exp(-c_{13}B_c)$, is always density-dependent, with B_c denoting the biomass of the cannibalizing part of the population. An example of how to model (positively and negatively) density-dependent harvesting is provided by Ernande et al. (2004).

Environmental variation

Inter-annual variability in the environment influences the life-history traits of all individuals in a population as a whole. For example, decreases in temperature or a reduction in food availability might depress somatic growth rates. This type of variability has evolutionary implications because it affects bet-hedging life-history strategies. Inter-individual environmental variation, by contrast, affects each individual in the population in a different way, often owing to small-scale environmental heterogeneity that influences individuals through local chance events. Environmental variation can also be temporally autocorrelated: for example, recruitment can be positively autocorrelated in time because of the inter-annual persistence of environmental conditions that affect demographic processes (Planque and Fredou 1999, Fogarty et al. 2001). A standard approach to incorporating such autocorrelation is based on first-order autoregressive models (e.g., Roughgarden 1975, Ottersen and Stenseth 2001, Fischer et al. 2009).

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In an eco-genetic model, the processes of growth, maturation, and reproduction can be modeled including phenotypic plasticity. Resource-limited growth – as described, e.g., by Equation 3f – is a form of passive plasticity and is a common feature in eco-genetic models, while adaptive growth plasticity may be included in more specialized models.

Growth-related maturation plasticity is very common and is included in eco-genetic models using maturation reaction norms (MRNs). A MRN represents the phenotypes of age and size at maturation as a function of an individual's juvenile growth rate (Stearns and Koella 1986). Changes in growth rates will cause a shift in the ages and sizes at maturation because the growth trajectories of individuals with different growth rates will then intersect the MRN at different positions. Evolution of a MRN reflects genetically-based changes in an organism's maturation schedule. This concept can be extended to account for the probabilistic nature of maturation by using probabilistic maturation reaction norms (PMRNs), which describe the length- and age-specific probabilities of maturation between one season and the next (Heino et al. 2002a, Dieckmann and Heino 2007). In an eco-genetic model, an individual's annual maturation probability can be calculated as

$$p_{\mathrm{m}} = [1 + \exp(-(l_a - l_{\mathrm{p50},a})/d_a)]^{-1} , \tag{4a}$$

where l_a is length at age a, $l_{\mathrm{p50},a}$ is the length at 50% maturation probability for age a (also known as the PMRN midpoint at age a), and the parameter d_a determines how steeply maturation probability changes around $l_{\mathrm{p50},a}$,

$$d_a = \frac{l_{\mathrm{u},a} - l_{\mathrm{l},a}}{\mathrm{logit}\, p_{\mathrm{u}} - \mathrm{logit}\, p_{\mathrm{l}}} . \tag{4b}$$

Here, $\mathrm{logit}\, p = \ln(p/(1-p))$, and p_{l} and p_{u} are probabilities – such as 25% and 75%, or 10% and 90%, respectively – used to characterize the lower and upper bounds of the probabilistic maturation envelope around $l_{\mathrm{p50},a}$. The envelope's width $l_{\mathrm{u},a} - l_{\mathrm{l},a}$ (also known as the PMRN

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width at age a) thus describes the range of lengths l_a over which maturation probability rises

from p_l to p_u at age a ; the smaller this width, the more deterministically the maturation

process is described by age and length. PMRNs with linear midpoint curves and constant

envelope width are described by

$$l_{p50,a} = i_P + a\, s_P \text{ and } d_a = d \ ,$$ (4c)

where i_P , s_P , and d are referred to as PMRN intercept, PMRN slope, and PMRN width,

respectively (Figure 2a shows an example of a linear PMRN).

Finally, while it is often convenient to assume an individual's gonado-somatic index to

be constant, assumptions implying phenotypic plasticity may readily be made to describe

populations in which reproductive investment strategies vary with the intake of resources.

Sex structure

Eco-genetic models may or may not incorporate sex structure. An absence of sex

structure is acceptable in models of hermaphrodites, models of species with little sexual

dimorphism in life history, or in generalized strategic models of life-history evolution. On the

other hand, modeling the sexes separately is necessary if there are large differences between

males and females, if evolving traits of interest exhibit sex-specific expression or inheritance,

or if sexual selection is strong.

Mating system

Three critical features affect the modeling of mating systems in eco-genetic models: (1)

the choice of mates, (2) the number of mates individuals have, and (3) the number of offspring

produced per mature individual. For (1), the simplest option is to model random mate choice;

this could be appropriate for broadcast spawners, for example, where actual mating pairs are

not formed. An alternative is assortative mating, which is common in nature, but often results

from preferential mating with like phenotypes. In general, assortative mating has two main

features that must be specified: the phenotypic character on which assortative mate choice is based (e.g., size), and the strength of assortativeness.

For (2), the offspring of a given female could be sired by many different males and vice versa; this would be the case for broadcast spawners, multiple-batch spawners, and species that mate with more than one partner during a reproductive season. Alternatively, some species might only mate with one other individual during a reproductive season (or even during their lifetime) and the eco-genetic model could be adjusted accordingly.

For (3), the fecundity f of a mature female can be made to depend on her reproductive investment, as measured by her phenotypic gonado-somatic index GSI_P, and body size,

$$f = \delta w_\mathrm{m} GSI_\mathrm{P} \tag{5}$$

where w_m is the somatic weight of the mature female and δ is the weight-specific oocyte density of the mature pre-spawning ovary. For males, a similar relationship could be used when large body size and high reproductive investment lead to higher reproductive success via a larger numbers of gametes produced and offspring sired.

All three elements above are related, and will need to be considered together, when implementing mating and reproduction in an eco-genetic model. Typically, details of mating systems are difficult to quantify in the wild and simplifying assumptions will thus often have to be invoked.

Implementation strategy

A basic consideration concerns the overall implementation of eco-genetic models. Specifically, eco-genetic models can be implemented either as compartment-based models or as individual-based models. In a compartment-based model, continuous state variables, including phenotypic and/or genetic trait values, have to be discretized into classes. The modeled population is then divided into different compartments, each of which represents one of all the many possible combinations of classes. The densities of individuals in these

compartments are then tracked through time. Most of the compartments, however, will usually be practically empty, leading to computational inefficiency. The decision to implement an eco-genetic model in this manner thus depends on the number of evolving traits and other state variables such as age, length, maturation status, and sex: inclusion of more than four or five continuous variables that have to be discretized will lead to such a vast number of compartments that a compartment-based implementation becomes impractical.

By contrast, in the individual-based implementation of an eco-genetic model (e.g., Dunlop et al. 2007, Thériault et al. 2008), the discrete or continuous variables characterizing each individual are tracked through time. Discretizing continuous state variables is therefore not required, and instead of tracking all possible types of individuals that could possibly exist, only types that are actually present are tracked, resulting in higher computational efficiency. This conclusion mirrors related suggestions that individual-based models are particularly valuable when there are several important dimensions according to how individuals in a population differ from one another (DeAngelis and Mooij 2005, Grimm and Railsback 2005, Grimm et al. 2005). In eco-genetic models, this is often the case because the details of phenotypic variation among individuals are crucial for the differential survival and reproductive success that drives evolution. It should be emphasized that, in principle, any given eco-genetic model can be implemented either compartment-based or individual-based, so that the choice of the most convenient implementation strategy is an entirely practical one, as both implementation strategies, when used correctly, will yield equivalent results.

Parameterization strategy

Like any other model in ecology, eco-genetic models can be either strategic or tactical. The goal of a strategic model is to understand a phenomenon and the underlying mechanisms, whereas the goal of a tactical model is to make specific predictions for a particular population or species. If tactical, an eco-genetic model can be parameterized with data collected for the population or species in question (e.g., Dunlop et al. 2007, Thériault et al. 2008). A strategic

model, on the other hand, has to be parameterized more generally, depending on the focus of research: if the goal is to address general questions of life-history evolution, it might not be relevant (or even helpful) to parameterize the model for any one population.

Values for some parameters will be more uncertain than for others, the worst case being an informed guess. A robustness analysis is then needed to check how model results are influenced by parameter uncertainties (see below). Alternatively, when model predictions can be compared with empirical observations, such as time series of life-history traits, an eco-genetic model can be used to estimate parameters that are unknown or uncertain, just as process-based population models are used for assessments of fish stocks (e.g., Frøysa et al. 2002). Parameters that are most likely given the data, together with their confidence intervals, can then be found through numerical optimization of the match between predictions and observations, or in a Bayesian fashion by identifying likely parameter values based on an eco-genetic model and plausible prior distributions of candidate values.

Robustness analysis

By definition, models simplify reality and purposefully omit extraneous variables and complicating assumptions. Eco-genetic models will often have a relatively strong reliance on, and coupling to, empirical data. Uncertainty in model predictions can arise depending on the availability and quality of key data used to parameterize the model and to support the structural assumptions on which the model is based. We recommend robustness analysis, also referred to as sensitivity analysis (Bart 1995, Drechsler 1998), especially for tactical applications of eco-genetic models. A parametric robustness analysis alters parameter values and thus quantifies the parameter's effect on model results. A structural robustness analysis adds, removes, or alters structural assumptions and quantifies the assumption's effect on model results. If important model results are strongly affected by uncertain model parameters or assumptions, further research efforts can be targeted accordingly.

Example: An Eco-genetic Model for Studying Harvest-induced Evolution

The applicability and utility of eco-genetic modeling is perhaps best appreciated by considering a concrete example. Below, we present a specific eco-genetic model we have developed for examining harvest-induced evolution (Figure 2). We developed this model based on recognizing the need for pursuing research directions in this area that can be investigated with the aid of an eco-genetic model, but not through previous approaches to evolutionary modeling. For example, while evidence of harvest-induced evolution has been documented in several species (e.g., Haugen and Vøllestad 2001, Coltman et al. 2003, Grift et al. 2003, Olsen et al. 2004), it is not yet clear how difficult it is to slow down or reverse the evolutionary impacts of harvest. Also, most theoretical work in this area (e.g., Law and Grey 1989, Heino 1998, Ernande et al. 2004, Baskett et al. 2005) has focused on maturation evolution, and it remains to be established what harvest-induced life-history syndromes should be expected as multiple traits undergo simultaneous evolution. The model below is parameterized for Atlantic cod (*Gadus morhua*), serving as a generic example for a late-maturing and potentially long-lived harvested species. Whenever possible, we have selected parameter values for populations in the northern part of the range of this widespread and diverse species (Brander 2005); the construction of population-specific models will be a natural next target for future research, but is not our aim here.

Model description

For our example, we extended the model by Dunlop et al. (2007) to study the effects of harvest on the simultaneous evolution of four life-history traits: two characteristics of the probabilistic maturation reaction norm (PMRN), in addition to somatic growth capacity and reproductive investment. The four traits are the genetic values of the PMRN intercept (i_G), PMRN slope (s_G), growth capacity (g_G), and gonado-somatic index (GSI_G). The eco-genetic

model involves annual updating, with events occurring at discrete time steps of 1 year. Owing

to the number of jointly evolving traits, an individual-based implementation was chosen.

Initial population. The initial population in our eco-genetic model consisted of 10,000

age-1 individuals (we found no difference when initializing the population with 500 individuals

and so we used a higher number to reduce the amount of simulation time needed for reaching a

stable population abundance). Genetic trait values in the initial population were assigned

randomly to individuals by drawing them from normal distributions with means equal to the

initial population mean of the trait in question, and variances σ_G^2 determined by the assumed

initial genetic coefficient of variation CV_G (initial standard deviation of genetic trait values

divided by their initial mean).

Phenotypic expression. The phenotypic expression of an individual's genetic traits was

based on two sources of environmental variation: inter-individual and inter-annual. For each

trait, the inter-individual environmental variance σ_E^2 was parsimoniously held constant through

time and was calculated based on the population's initial heritability h^2 and genetic variance

σ_G^2 for that trait, $\sigma_E^2 = \sigma_G^2 (h^{-2} - 1)$. Each year, an individual's phenotypic values (i_P, s_P,

GSI_P, and g_P) for all four genetic traits (i_G, s_G, GSI_G, and g_G) were drawn from a normal

distribution with means equal to the individual's genetic trait values and variances equal to σ_E^2

calculated for the trait in question. Further inter-annual environmental variation in growth

resulted from density-dependent resource limitation (Equation 3f). Note that although

heritability is assumed to be 0.2 in the initial year (Table 2), it becomes an emergent property

of the model in subsequent years.

Maturation and growth. The probability of maturation for an immature individual in a

given year was calculated from Equations 4a-c. Once an individual became mature, it entered

the reproductive stage of life, with reproduction occurring annually after the growing season.

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The annual somatic growth of individuals followed the Lester et al. (2004) growth model: immature growth was linear and with annual phenotypic length increments g_D, whereas mature individuals grew according to Equation 2a.

Reproduction and inheritance. The fecundity of each female was a function of her phenotypic gonado-somatic index and body weight (Equation 5). The number of surviving offspring (recruits) produced by the population was determined from a Beverton-Holt model (Equation 3a). For each offspring, a mature male and female were randomly drawn with replacement as parents (thus assuming random mate choice), with the probability of each being chosen as a parent being proportional to their gonad weight. We took this approach because individuals with large gonads (owing to their large body size and/or GSI_p) are expected to produce a higher numbers of gametes (eggs or sperm) and therefore more offspring. Also, with this approach, a given female may mate with several males and a given male may mate with several females, in accordance with the expectation for batch spawners such as Atlantic cod (McEvoy and McEvoy 1992, Kjesbu et al. 1996).

Each offspring inherited the evolving traits of its parents by receiving randomly drawn genetic trait values from normal distributions with means equal to the mid-parental trait values and variances equal to half of the trait's genetic variance in the initial population (thus assuming a constant segregation-recombination kernel). For the purposes of this example model, we decided not to add genetic trait covariances because there is virtually no empirical data from which such covariances could be estimated. Sex was assigned randomly at birth assuming a 1:1 primary sex ratio.

Natural mortality. Natural mortality was introduced through a trade-off between growth and survival (Equation 2d). An additional background natural mortality probability m_b was used to raise the total instantaneous rate of natural morality to the 0.2 yr^{-1} commonly assumed for cod (Gunderson 1997, ICES 2007a). Mortality probabilities in the model were

implemented as Bernoulli trials: if a random number drawn between 0 and 1 was less than or equal to the mortality probability, the individual died and was removed from the population. Natural mortality during the juvenile phase also included density-dependent offspring mortality (Equation 3a).

Harvest mortality. The model was run for 2000 years prior to harvest so that the population abundances and evolving traits could approach a pre-harvest equilibrium (we verified the stationarity and stability of this equilibrium by running some simulations for 1 million years). After 2000 years, size-selective harvest mortality was applied for 100 years and then a harvest moratorium was implemented for 100 years. During the years of harvesting, we investigated an exploitation pattern with a constant harvest rate, in which all individuals above a minimum length limit had a given annual probability of being harvested. We ran the model for different minimum length limits (between 20 cm and 100 cm in increments of 10 cm) and different annual harvest probabilities (0, 0.2, 0.4, 0.5, and 0.6).

Parameterization. We parameterized the model for Atlantic cod, a species characterized by high fecundity, intermediate age at maturation, and low natural mortality associated with long potential lifespan (Table 2). Deliberately, the model presented here is not parameterized for any particular cod stock, but the chosen parameters best describe cod populations in the northern part of the species' range, such as those in the Barents Sea and off Newfoundland–Labrador.

Robustness analysis. In addition to testing the effects of different minimum length limits and harvest probabilities, we also tested the robustness of model results to changes in several other functions and parameters. These included the growth-survival trade-off (Equation 2d), the stock-recruitment relationship (Equation 3a), the strength of density-dependent growth (Equation 3f), and the assumed genetic coefficient of variance CV_G in the initial population (see Appendix 1 for further details).

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Response to harvest

Harvest induced an evolutionary shift of the PMRN to younger ages and smaller sizes at maturation, indicated by the decreasing intercept of the PMRN (Figure 3). The direction of evolution in the PMRN was similar to that observed for harvested populations in the wild (Grift et al. 2003, Olsen et al. 2004, Mollet et al. 2007) and predicted by previous models (Ernande et al. 2004, Dunlop et al. 2007). In contrast, the PMRN slope did not evolve in response to harvest. We also observed evolution of smaller genetic growth capacity (Figure 3). As no published model has previously examined the simultaneous evolution of genetic growth capacity and PMRNs, it is pertinent to point out that a dramatic downward shift of the PMRN occurred even when growth capacity evolved simultaneously with the PMRN.

Reproductive investment (GSI) increased in response to size-selective harvest (Figure 3). This pattern was expected because when mortality rates are substantial, evolution favors those individuals that sacrifice future growth for higher investment into current reproduction (Roff 1992, Heino and Kaitala 1996, Lester et al. 2004). However, like genetic growth capacity, GSI changed by only a small amount. Instead, harvest had the largest impact on the PMRN intercept. This finding is in agreement with empirical accounts of downward shifts in the PMRN (Grift et al. 2003), but no clear trend in the GSI (Rijnsdorp et al. 2005), of harvested North Sea plaice (*Pleuronectes platessa*).

The evolution of traits was accompanied by changes in population abundance, biomass, and phenotypes. Harvest caused a reduction in biomass of 74% and a reduction in abundance of 14% (means for 30 repeated model runs). In addition, age at maturation and length at maturation decreased, while the phenotypic length increment first increased and then decreased (Figure 3). The phenotypic changes occurred much quicker and sometimes in the opposite direction as the genetic changes, thereby partially masking the underlying evolutionary responses. Managers and resource stakeholders must be concerned about the possibility that

masked evolutionary shifts induced by harvest could be difficult to detect during intermediate periods, while eventually still causing diminished economic returns.

The robustness analysis indicated that factors such as density-dependent growth and recruitment, genetic variance, and life-history tradeoffs did have an effect on the amount of fisheries-induced evolution, thus pointing to the importance of including such features in evolutionary models designed to make quantitative predictions for specific populations (Appendix 1). However, the qualitative predictions of our model were invariant with respect to these features: harvest had the largest impact on the PMRN, causing it to shift downwards, while at the same time inducing evolution of growth capacity and reproductive investment (Appendix 1).

Response to a moratorium

Perhaps the most worrisome finding of our analysis was that the recovery of life-history traits from harvest-induced evolution during a moratorium was slow to non-existent. The rate of change in traits when harvest was applied was usually considerably faster than the rate of reversal once harvest ceased (Figure 3). The striking difference in evolutionary rates during harvest, as opposed to once harvest was halted, can be attributed to the strong harvest-induced selection imposed on the population when harvest occurred, compared to the much weaker natural selection which acted when harvest was absent. A similar asymmetry was already demonstrated in simpler adaptive dynamics models (Law and Grey 1989). Our results further show that this slow reversal was not the result of reduced genetic variance: for example, the genetic variance in the PMRN intercept decreased only negligibly (by 2.5%) during 100 years of harvest. Future work could aim at uncovering whether the traits will fully recover given an even longer moratorium, or if they will reach an alternative stable state (e.g., de Roos et al. 2006). The lack of recovery in evolving traits predicted from our model may provide one explanation as to why several commercial stocks of fish have failed to rebound following moratoria (e.g., Hutchings 2000).

Response to different harvesting patterns

For the PMRN intercept and GSI, an intermediate length limit caused the largest amount of evolution (Figure 4). Most intriguing was that the effect of harvest on the genetic growth capacity qualitatively depended on the minimum length limit. When the minimum length limit was set well below the length at maturation, harvest induced an increase in genetic growth capacity, whereas the opposite effect was observed for higher minimum length limits (Figure 4). These complex responses were likely the result of selective pressures acting on the age and size at maturation. When the length limit was small, more immature individuals were captured and selective pressures favored those individuals that matured prior to being harvested; in this case, larger genetic growth capacities evolved because individuals growing faster matured earlier in life. When length limits targeted primarily mature individuals, slower growth was selected for because individuals had already matured and there was a fitness advantage to avoiding the minimum length limit by growing slower. Although it has been argued that fishing is likely to select for smaller growth capacities (e.g., Conover and Munch 2002), our results show that this prediction is more complicated than has been commonly appreciated.

Finally, and not surprisingly, increasing the constant harvest probability caused an increase in the evolutionary response: the genetic PMRN intercept shifted noticeably downwards (Figure 5), while the genetic GSI became slightly higher (after 100 years of fishing it equaled 0.119, 0.122, 0.125, and 0.127 for harvest probabilities 0, 0.2, 0.4, and 0.6, respectively), and the genetic growth capacity became slightly lower (after 100 years of fishing it equaled 12.9, 12.9, 12.6, and 12.0 cm for harvest probabilities 0, 0.2, 0.4, and 0.6, respectively). At the same time, the phenotypic length increments became larger (Figure 5), again masking the underlying genetic change in growth capacity. These results clearly indicate that reducing harvest rates is one viable management measure for reducing the evolutionary response to fishing.

Discussion

Eco-genetic modeling is an integrative tool for studying life-history evolution, in particular at contemporary timescales and in realistically complex ecological settings. Using an eco-genetic model to examine the processes that create life-history variation offers several advantages. First, eco-genetic models can describe the simultaneous evolution of multiple life-history traits in realistically structured populations. Second, eco-genetic models predict the actual rate of evolutionary change, crucially increasing the applicability of predictions. Third, eco-genetic models are easily applied to systems with density-dependent and frequency-dependent selection, even when such selection pressures are strong. Fourth, eco-genetic models are readily used, as a special case, for exploring ecological dynamics when no evolution of life-history traits occurs; this facilitates the identification of evolutionary effects. We contend that through this novel combination of features, eco-genetic modeling enables a fuller appreciation of the mechanisms and complexities governing a population's adaptation to its environment and to anthropogenic perturbations.

Development of eco-genetic models is currently progressing in two areas: (i) scientific analyses of fisheries-induced evolution and (ii) development of the underlying modeling methodology. These two areas of research go hand-in-hand because a rigorous methodology is required for adequately examining specific questions about fisheries-induced evolution through model-based studies. The two previously published eco-genetic models included methodological advancements, but were meant to explore specific scientific questions about the effects of mortality on the evolution of life-history traits. The first study (Dunlop et al. 2007), investigated the effect of selective mortality on evolution of the slope and intercept of the probabilistic maturation reaction norm of smallmouth bass populations. The second study (Thériault et al. 2008), explored the effect of fishing on the evolution of anadromy in brook

charr. The underlying models advanced methodology through the inclusion of multiple traits describing the evolution of reaction norms (of maturation in the first study and of migration in the second) over contemporary timescales (tracing traits on an annual basis over the course of 100 years). Other specific scientific questions related to fisheries-induced evolution currently being explored based on eco-genetic modeling include the influence of evolution on recovery, the efficacy of marine protected areas, the importance of spatial stock structure, sexual size dimorphisms, and the interplay between fisheries-induced and sexual selection.

We see eco-genetic models as being used to address at least four different topics in the coming years. These topics are listed here because, in our assessment, the current knowledge gaps hold particular promise for being addressed through applications of eco-genetic models. First is the modeling of sex-specific male and female life histories and resultant sexual dimorphisms. Most previous life-history models, including the one presented as an example above, include no or only rudimentary sex structure and usually focus on the female life history. This simplified treatment naturally poses a problem when there are large differences between males and females. In such situations, one will also often try to understand the impact of harvesting on the exploited population's sex ratio. The second topic is the modeling of the evolutionary dynamics of trait covariances (i.e., technically speaking, of the G-matrix; see the section 'Inheritance model'). The largest challenge here is that relatively little empirical data is available on these covariances in the wild, which is why many eco-genetic models will assume them to be absent. Evolution of genetic variance-covariance matrices in response to natural selection is an area of active research (Steppan et al. 2002, Jones et al. 2003) and one that could readily be explored more thoroughly with the help of eco-genetic models. Such applications could also explore how anthropogenic selection pressures influence genetic variance-covariance matrices and how, in turn, genetic covariances affect selection responses to anthropogenic pressures. The third topic is the linking of eco-genetic models with other types of models. The output of an eco-genetic model could easily be interfaced with stock-

assessment models, socio-economic models, or models for decision analysis, increasing the utility of eco-genetic models in the wider context of resource management. Model interactions across such interfaces will often be bidirectional, with the biological model driving socio-economic or behavioral states, and vice versa. The fourth topic of potential promise is the use of eco-genetic models in evolutionary impact assessments (EvoIA). EvoIAs were introduced as a tool for investigating how alternative management measures change the impacts of fisheries-induced evolution (ICES 2007b; Jørgensen et al. 2007). Prospective EvoIAs project the impacts of evolution on utility metrics (such as profit, yield, or employment) into the future and thus require quantitative models that can predict evolutionary transients on contemporary timescales (Jørgensen et al. 2007); eco-genetic models provide an ideal platform for this type of application.

Tactic eco-genetic models are tightly linked to, and rely on, empirical knowledge guiding the selection of model structure and parameterization. Important empirical data for the parameterization of such models includes: (i) time-series data to estimate stock-recruitment relationships and the density dependence of growth; (ii) data on life-history traits, such as maturation schedule, somatic growth capacity, and reproductive investment; (iii) general knowledge pertaining to a population's life-cycle, including mating and spawning behavior; (iv) genetic data for quantifying generic variances, covariances, and heritabilities; and, for exploited populations, (v) harvest statistics such as catch, harvest rate, effort, and selectivity. While this list summarizes the information most commonly used in an eco-genetic model with a tactic emphasis, not all of these data are needed for each and every eco-genetic model, because data requirements will naturally vary with the focal questions being asked.

Resources and time are not always available to collect all the information that could fruitfully be integrated in eco-genetic models. Fortunately, there are several options available for dealing with missing or uncertain data in eco-genetic modeling. Structural assumptions and quantitative parameters from closely related species or populations can often be substituted,

and an extensive robustness analysis can be carried out to evaluate the implications for model predictions. The need for studying such implications based on a quantitative modeling approach will often be preferable to the inability to investigate them at all. Alternatively, various forms of model fitting can be applied, as in stock-assessment models, for estimating values of unknown parameters (Hilborn and Walters 1992). If only a few parameters are unknown for a specific population, the criterion of consistency between extensive empirical observations and theoretical predictions from whole-life-cycle modeling can indeed serve as a powerful tool for estimating such unknowns. For example, the predictions of an eco-genetic model can be compared with available empirical data for different values of genetic variances and heritabilities, and those values giving the best fit could be identified. A pattern-oriented modeling approach (Grimm and Railsback 2005), which allows researchers to identify those key patterns in a system that the model should reproduce, can of course also be applied to eco-genetic modeling. Alternative hypotheses can then be formulated (e.g., about which mechanism is driving the key patterns) and tested by comparing model output with observed patterns. It is our experience that although tactic eco-genetic models can be data-hungry, one of their strong assets is that they can seamlessly integrate diverse levels of quantitative detail, by taking full advantage of comprehensive empirical information where available and combining this with more generic assumptions where needed.

While eco-genetic models have potentially wide-ranging applications in life-history theory and ecosystem management, they have already proven their worth in the more specific context of studying fisheries-induced evolution. The number of studies concluding that fisheries-induced evolution is a likely candidate for explaining components of observed life-history changes is now quite large (see recent reviews by ICES 2007b, Jørgensen et al. 2007, Kuparinen and Merilä 2007, Fenberg and Roy 2008, Heino and Dieckmann 2008, Hutchings and Fraser 2008). The strength of evidence afforded by these empirical studies remains debated, as it is never possible to exclude with certainty that observed phenotypic changes

were caused by unaccounted for factors in a population's environment (see, for example, Hilborn 2006, Marshall and Browman 2007, Browman et al. 2008, Heino et al. 2008, Jørgensen et al. 2008, Kuparinen and Merilä 2008). In this context, quantitative modeling assumes a particularly important role. The eco-genetic model presented in this paper strengthens the theoretical evidence that fisheries-induced evolution can account for a significant component of observed trends in the life-history traits of exploited stocks.

Model-based support in the evolutionary interpretation of empirical patterns naturally depends on how realistic the utilized model is. All models are gross simplifications of reality, and it will always remain open to discussion how realistic a model needs to be before it can credibly support empirical hypotheses. We would thus like to emphasize that the eco-genetic model presented as an example above accounts for what, in the context of modeling multi-trait life-history evolution, is probably an unprecedented degree of ecological detail and, hopefully, realism. This includes, in particular, environmental variability, phenotypic plasticity, and density-dependent growth, all of which have been invoked to explain life-history changes in exploited fish populations, and indeed affect life-history changes in our model. For example, the reduction of the population biomass as a result of fishing caused higher food availability and faster growth rates; this resulted in an earlier age at maturation. The downward evolutionary trend in the PMRN midpoint also contributed to earlier maturation. Thus, genetic and environmental factors jointly influenced the trend in age at maturation. This also is likely to be true for the wild Atlantic cod stocks that have shown trends in maturation schedule and PMRN midpoints (Heino et al. 2002b, Barot et al. 2004, Olsen et al. 2004). In this way, eco-genetic models can help us understand how multiple factors, including evolution, contribute to fishing-induced changes, past and future.

In summary, an eco-genetic model incorporates important life-history principles such as trade-offs between growth, reproduction, and survival, as well as population structure, density dependence, frequency dependence, phenotypic plasticity, stochasticity, and inheritance.

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Inclusion of these features (i) allows a tight linkage between eco-genetic models and empirical data, (ii) enables the prediction of both genetic and phenotypic transients, and (iii) permits examination of the speed of evolution on empirically relevant and realistic timescales, thereby increasing the applicability and utility of life-history predictions.

Acknowledgments

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Eco-genetic models

Table 1. Choices and guidelines for building an eco-genetic model. Listed choices are usually not exhaustive, but highlight the most commonly considered options.

Building blocks	Choices	Guidelines for selection
Evolving traits	Standard set of traits for maturation, growth, and reproductive effort	Recommended for general investigations of life-history evolution.
	Other sets of traits	More specific investigations may require other traits, e.g., mate-choice traits for describing sexual selection. Parameterization will be easier for models with fewer evolving traits. Too few evolving traits, however, may unduly constrain the evolutionary process.
Inheritance model	Allelic	Recommended when inheritance is known to be determined by only a few loci. Neutral loci can be used to track patterns of relatedness and genetic diversity.
	Quantitative genetic	Recommended for quantitative traits, including essentially all life-history traits.
Segregation-recombination variances and covariances (when assuming quantitative genetic inheritance)	Variances and covariances are constant	Implies that segregation-recombination variances and covariances change neither with time nor with parental distance.
	Variance and covariances equal half of parental values	Time-honored assumption: segregation-recombination variance can change with time, but not with parental distance.
	Standard deviations equal half of parental distances	Realistic, but not widely used: segregation-recombination variances and covariances can change with time and increase with parental distance.
Growth model	Lester et al. (2004)	Recommended default choice. Applies to organisms in which somatic and gonad growth occur sequentially during each season and in which gonad weight does not contribute to weight acquisition.
	Roff (1983)	Similar to the Lester et al. model, but not generally recommended. Applies only to organisms in which gonad weight contributes to weight acquisition.
	West et al. (2001)	Alternative to the Lester et al. model. Recommended if the latter does not describe growth adequately (e.g., when juvenile growth is not linear in length).
Density dependence	Newborn mortality	Density dependence in many populations is generally believed to be most important for early life stages. This is typically modeled as density-dependent newborn mortality.
	Growth	Resource-limited growth is recognized as being widespread in many populations. Inclusion of this process critically affects predictions on size structure and yield.
	Cannibalism	Intraspecific predation is important for juvenile age groups in many populations.
	Harvesting	Most harvesting regimes imply density-dependent harvesting mortality.
	Depensation	Positive density dependence (Allee effects) critically affect population dynamics at low densities.

Eco-genetic models

Environmental variation	Inter-annual	Inter-annual variability is ubiquitous and crucially affects strategies involving bet-hedging.
	Inter-individual	Inter-individual variability is ubiquitous and can be important for intraspecific interactions.
	Temporal autocorrelation	Positive temporal autocorrelations are a common feature especially of aquatic environments.
Phenotypic plasticity	Growth	Resource-limited growth is a trivial but omnipresent form of (passive) plasticity. In addition, adaptive growth plasticity may occur.
	Maturation	Growth-related plasticity in maturation is ubiquitous: accounting for this through the use of maturation reaction norms is thus recommended.
	Reproduction	Reproductive effort will often depend on resource intake. This can be included through reaction norms, which, however, may be difficult to parameterize.
Sex structure	Only one sex	Acceptable simplification when male and female life histories are not too different, so that the two sexes possess the same demographic and genetic structure. Also applicable for hermaphrodites. Two one-sex models together can describe sexually dimorphic populations, provided that trait expression is sex-limited and sexual selection is weak.
	Males and females	Required if there are important differences in male and female life histories, trait expression is sex-specific, or sexual selection is strong.
Mating system: mate choice	Random mating	Simple assumption that will usually serve as a null model in the absence of better information.
	Assortative mating	Assortative mating is ubiquitous, but quantitative details often remain unknown. The incorporation of assortative mating will be critical when sex-specific life histories are considered in conjunction with strong sexual selection.
Mating system: mate number	One mate per season	Appropriate for monogamous species.
	More mates per season	Appropriate for multiple-batch or broadcast spawners and for polyandrous or polygynous species.
Mating system: offspring number	Sexes treated equally	Applies if there is no sex structure. Typically, the number of offspring produced per parent individual will depend on its body size and current reproductive investment.
	Sexes treated differently	Important when it is known that the determinants of reproductive success differ between males and females.
Implementation strategy	Individual-based	Very flexible approach recommended as the first choice. Only computationally feasible option when more than about four continuous individual state variables are needed or a complex allelic inheritance model is used.
	Compartment-based	Applicable option when only a few continuous state variables are needed for characterizing individuals.
Parameterization strategy	Strategic	Recommended for establishing generalizable insights, transcending the idiosyncrasies of specific populations.
	Tactic	Required for conducting eco-genetic investigations of specific populations.
Robustness analysis	Parametric	Recommended to systematically explore the effect of parameter values on model predictions.

Eco-genetic models

	Structural	Recommended to investigate how specific mechanisms or assumptions influence model predictions.

Table 2. Parameter values for an eco-genetic model of Atlantic cod.

Description	Symbol	Equation	Value	Source
Initial mean genetic PMRN intercept (cm)	$\bar{i}_G$	–	93 (90)	(1)
Initial mean genetic PMRN slope (cm yr^{-1})	$\bar{s}_G$	–	–0.052 (–0.052)	(1)
Initial mean genetic GSI	$\overline{GSI}_G$	–	0.12 (0.12)	(1)
Initial mean genetic growth capacity (cm)	$\bar{g}_G$	–	12.8 (12.9)	(1)
Initial genetic coefficient of variation	CV_G	–	0.08	(2)
Initial heritability	h^2	–	0.2	(2)
GSI conversion factor	γ	2a	0.578	(3)
Length at age 0 (cm)	l_0	–	0	(3)
Length-weight allometric constant (g cm$^{-\alpha}$)	μ	–	0.01	(4)
Length-weight allometric exponent	α	–	3	(4)
Maximal growth increment (cm)	g_{max}	2d	80	(1)
Maximal fraction of surviving offspring	s_0	3a	$5.3 \cdot 10^{-2}$	(5)
Beverton-Holt constant	c_1	3a	$1.2 \cdot 10^{-6}$	(6)
Growth-biomass constant (g^{-1})	c_{11}	3f	$1.02 \cdot 10^{-8}$	(7)
Growth-biomass exponent	c_{12}	3f	0.3	(7)
PMRN width (cm)	d	4c	25.9	(8)
Weight-specific oocyte density (g^{-1})	δ	5	$4.4 \cdot 10^3$	(9)
Background natural mortality probability	m_b	–	0.02	(10)

Eco-genetic models

Numbers in brackets under 'Value' are the mean pre-harvest equilibrium trait values (reached after 2000 years without harvest and averaged over 30 independent model runs). PMRN is the probabilistic maturation reaction norm, with a width defined by the 25th (lower) and 75th (upper) percentiles of maturation probability ($p_l = 0.25$ and $p_u = 0.75$). GSI is the gonado-somatic index. Sources are as follows: (1) Set so that the pre-harvest equilibrium of evolving traits is reached within 2000 years and values are within empirical ranges for Atlantic cod reported for PMRNs (Heino et al. 2002b, Olsen et al. 2004), GSIs (Lloret and Ratz 2000, Rose and O'Driscoll 2002, McIntyre and Hutchings 2003), and growth rates (Marshall et al. 2004, Olsen et al. 2005, ICES 2007a). (2) Within the range reported by Mousseau and Roff (1987) and Houle (1992). (3) Lester et al. (2004). (4) Produces a relationship between fecundity and body length within the range reported by McIntyre and Hutchings (2003). (5) Estimated by nonlinear least-squares regression from data presented in Marshall et al. (2000). (6) Estimated as for (5) and then scaled so that population abundance at pre-harvest equilibrium is computationally manageable (ca. 20,000 individuals). (7) Set so that the range of phenotypic growth rates predicted by the model is within empirical ranges for Atlantic cod (Marshall et al. 2004, Olsen et al. 2005, ICES 2007a). (8) Olsen et al. (2005). (9) Thorsen and Kjesbu (2001). (10) Set so that the total natural annual mortality probability is ca. 0.18, corresponding to an instantaneous mortality rate of ca. 0.2 yr^{-1} (Gunderson 1997, ICES 2007a). A robustness analysis of several model parameters is presented in Appendix 1.

Figure Captions

Figure 1. An overview of eco-genetic modeling.

Figure 2. Schematic representation of the example eco-genetic model showing various functions used. (a) A hypothetical probabilistic maturation reaction norm (PMRN) of an individual showing the midpoint curve (continuous line) and envelope (dotted lines) (Equation 4c). (b) Density-dependent growth function (Equation 3f). (c) Example of an individual's mean growth trajectory (Equation 2a). (d) Relationship between fecundity and body length (Equation 5). (e) Stock-recruitment relationship (Equation 3a). (f) Normal distribution of offspring genetic trait values for a given pair of parents. (g) Normal distribution of phenotypic trait values based on a given genetic trait value and environmental variance. (h) Trade-off between genetic growth capacity and mortality probability (Equation 2d). (i) Size-dependent harvest probability, rising from 0 to the assumed harvest level for individuals above the minimum length limit.

Figure 3. The response to 100 years of harvest (grey area) followed by 100 years of harvest moratorium (white area) in Atlantic cod. Genetic traits (top four panels) respond gradually to changes in the environment, whereas phenotypic traits (bottom four panels) display rapid and abrupt responses. PMRN = probabilistic maturation reaction norm; GSI = gonado-somatic index. Minimum length limit was 60 cm, harvest probability was 0.5, and results were averaged over 30 independent model runs.

Figure 4. Effect of the minimum-length limit on the evolution of life-history traits in Atlantic cod. Panels show the percentage change in the evolving traits after 100 years of harvesting, relative to the year before harvesting started. To make the scale of the horizontal axis identical for all panels, the percentage change in the PMRN slope was multiplied by 10 (necessitated by particularly slow evolution). PMRN = probabilistic maturation reaction

norm; GSI = gonado-somatic index. Harvest probability was 0.5 and results were averaged

over 30 independent model runs.

Figure 5. Probabilistic maturation reaction norms (PMRNs) for Atlantic cod after 100 years

of harvest. Panels depict the probability of maturation in grayscale rising from just above 0

(white) to just below 1 (black). The dashed line is the PMRN midpoint curve (defined by the

length at age with 50% maturation probability), while the continuous line is the mean

immature phenotypic growth curve. For reference, the filled circle indicates where the mean

growth trajectory intersects the lower bound of the maturation envelope (above which

individuals mature with a probability in excess of 25%). Minimum length limit was 60 cm

and results were averaged over 30 independent model runs.

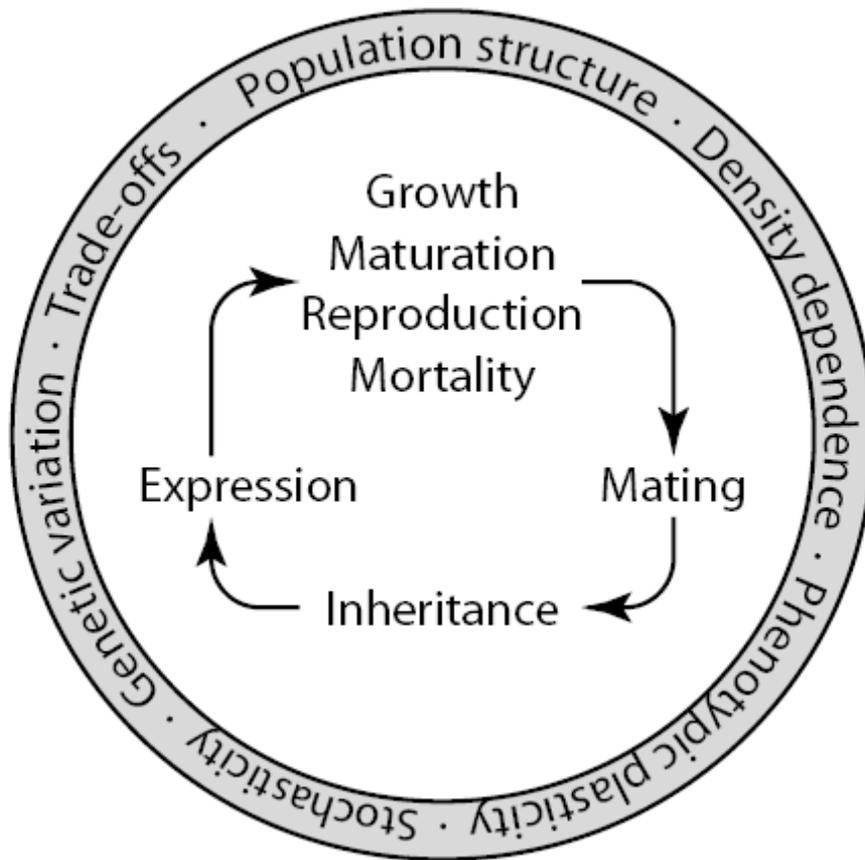Eco-genetic models
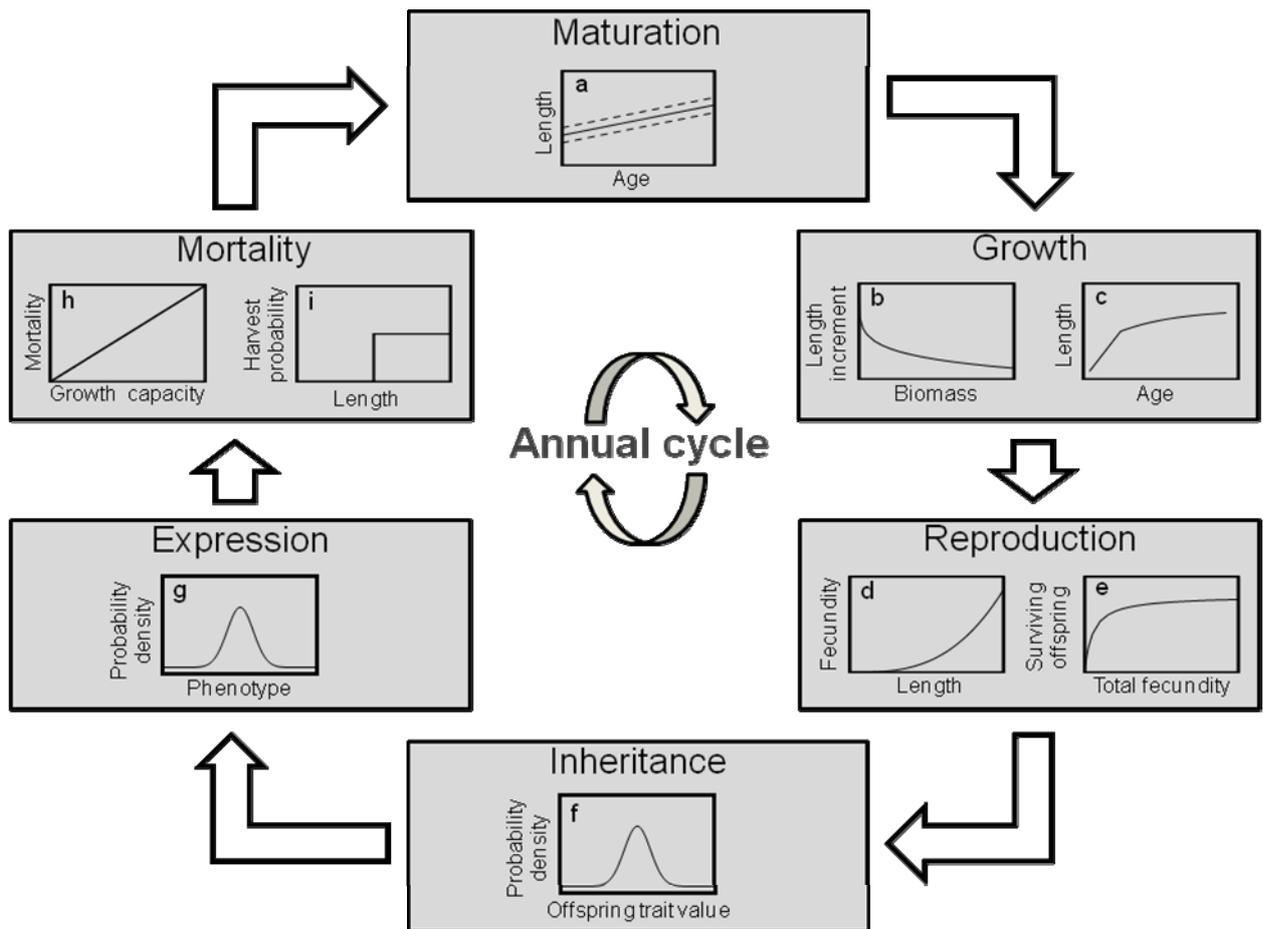
Figure 1.

Eco-genetic models
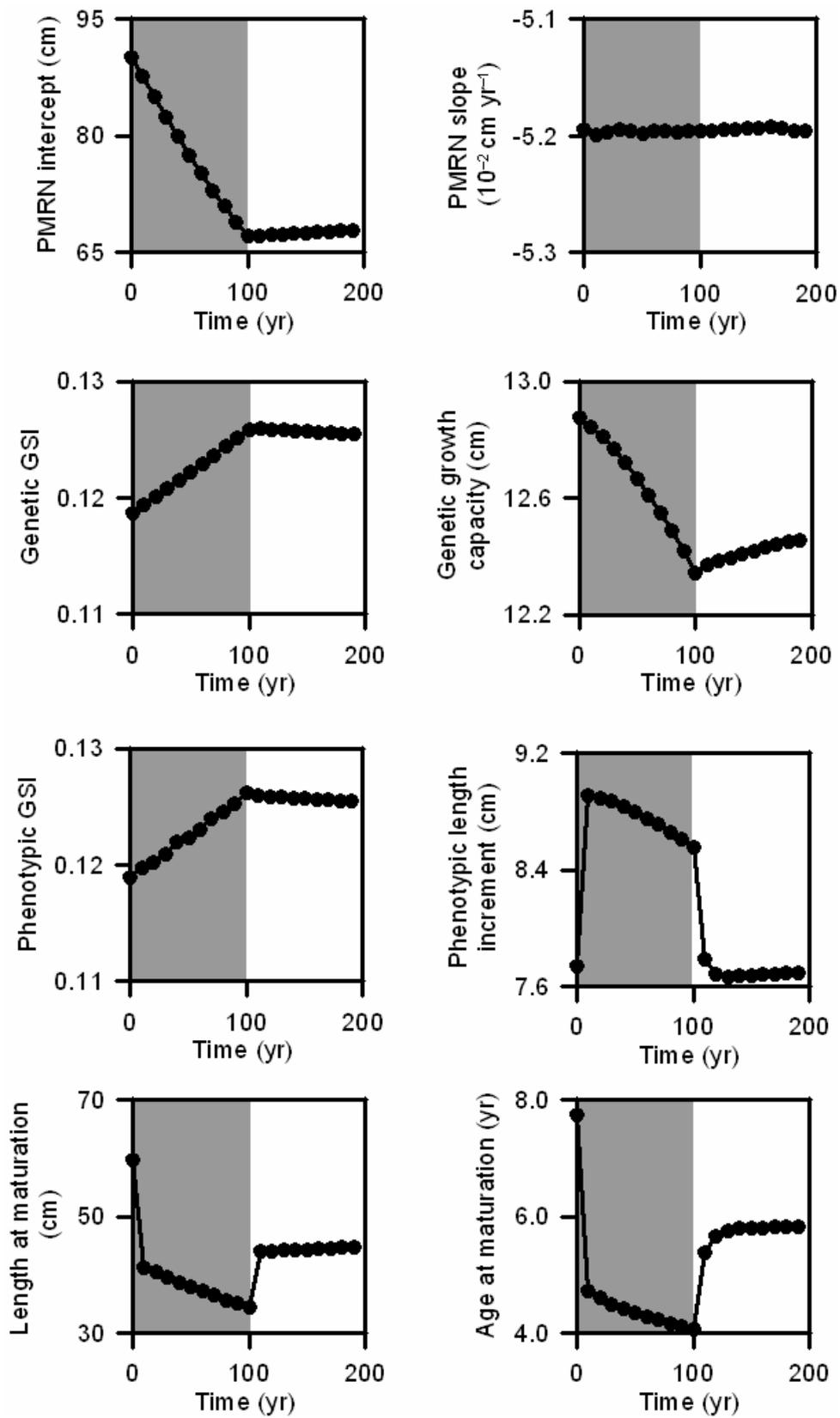
Figure 2.

Figure 3.

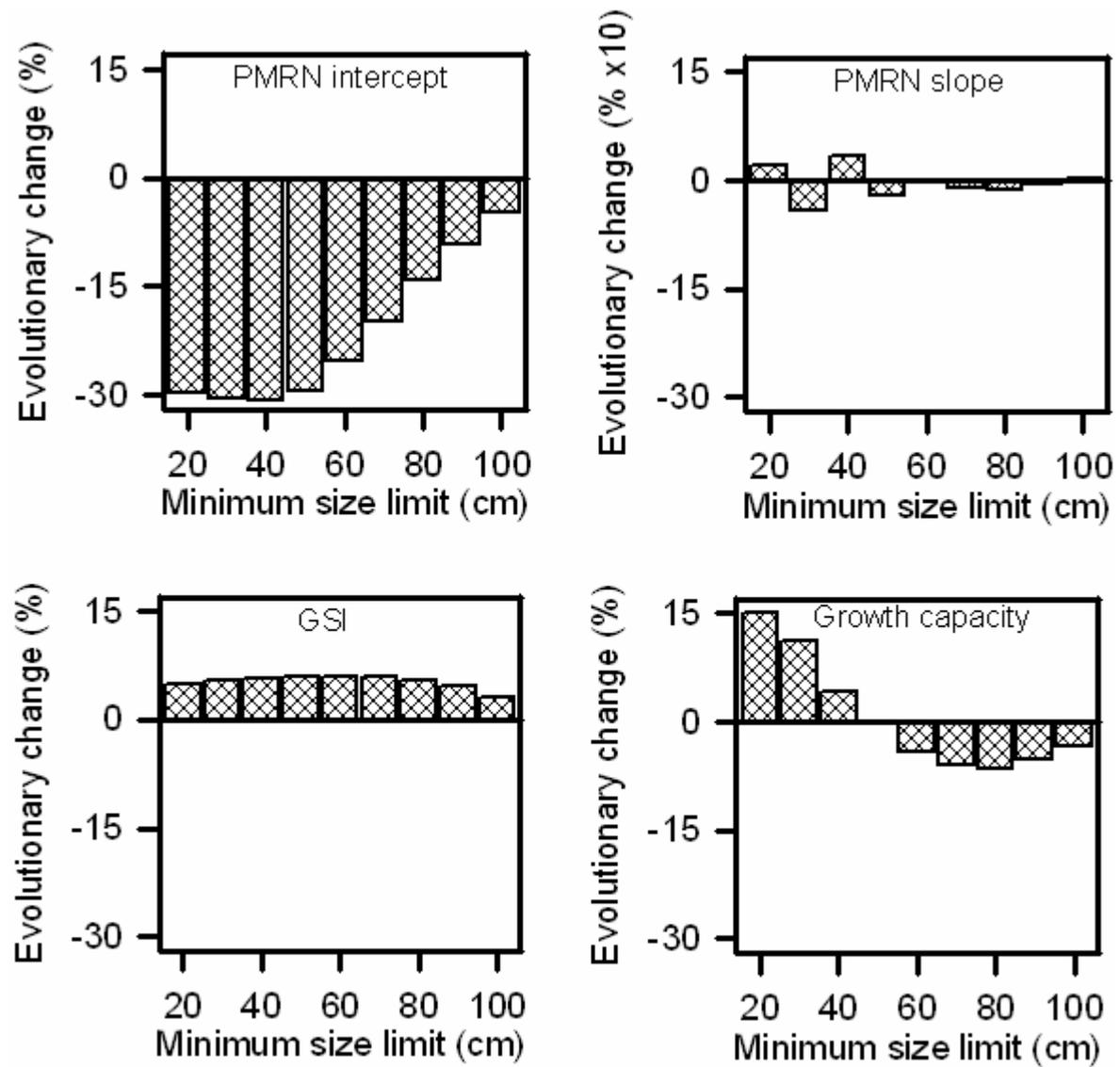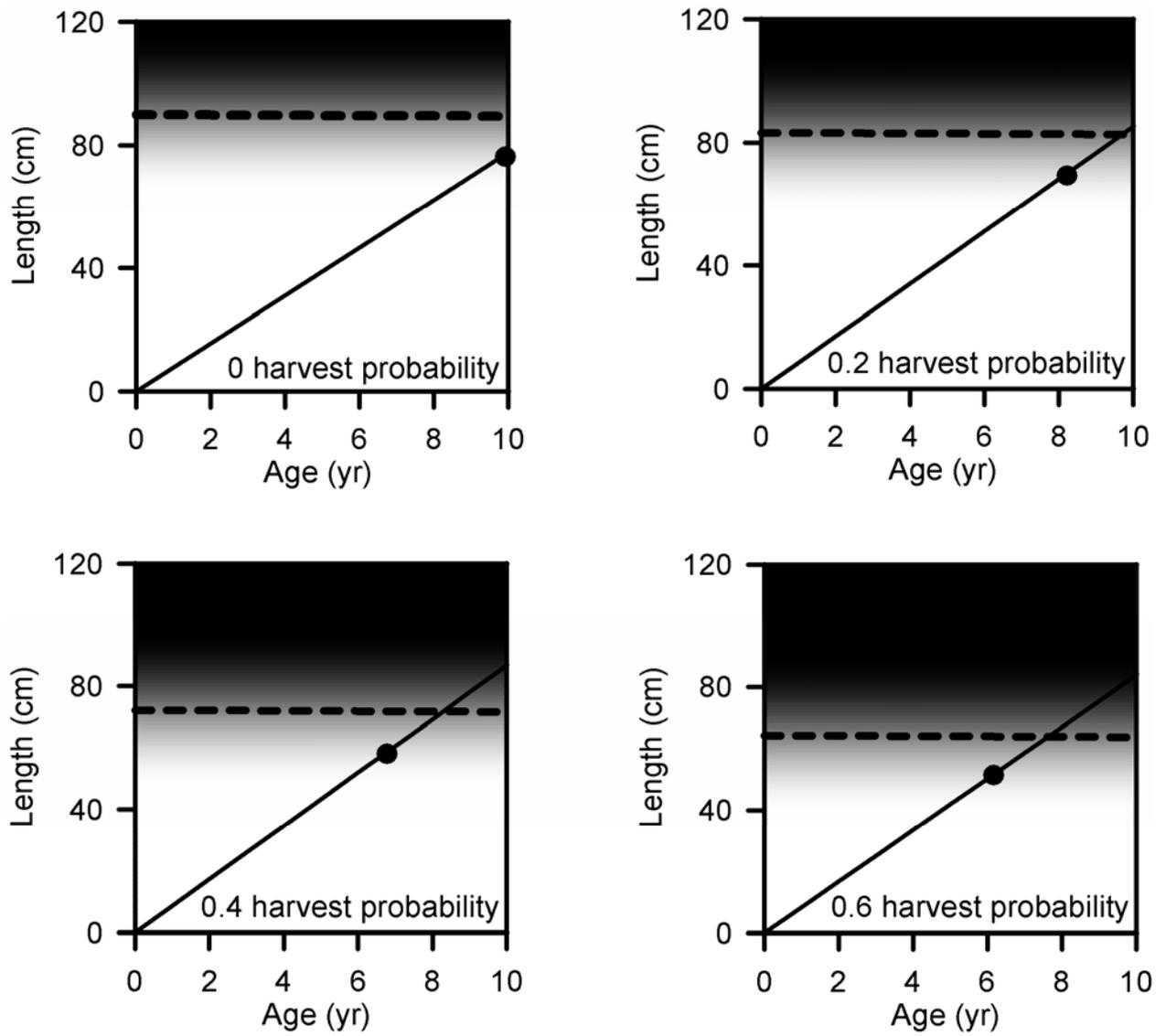Eco-genetic models

Figure 4.

Figure 5.

Appendix 1: Robustness analysis

In addition to testing the effects of different minimum length limits and harvest probabilities as described in the main text, we also tested the robustness of model results to changes in several other functions and parameters.

The growth-survival trade-off (Equation 2d) was expected to influence growth evolution: raising g_{max} reduces the severity of the trade-off and causes a lower cost of faster growth. Therefore, not surprisingly, raising g_{max} elevated the genetic growth capacity after 100 years of harvest (Figure A1a).

For the other robustness tests, we focused on effects on the PMRN intercept, because this trait consistently showed a large evolutionary response to harvest. Nevertheless, detailed results for all traits are presented in Table A1. The magnitude of evolution was positively correlated with changes in the parameter s_0, which determines the density-dependent mortality of newborn offspring (Equation 3a); however, the overall difference in the position of the PMRN after 100 years of harvest was small (Figure A1b). Higher values of s_0 produce larger population abundances, which, in turn, produce smaller phenotypic length increments; possibly, there is then compensation in the evolution of the PMRN in response to this slower growth.

We also tested the effect of changing the relationship describing density-dependent growth by varying the parameter c_{11} (Equation 3f) between 0 (density-independent growth) and $21.5 \cdot 10^{-8}$ g^{-1}(causing a strong reduction in growth with increasing population biomass). We observed an increase in the evolutionary response in the PMRN intercept when c_{11} was increased (Figure A1c), so that the slowest evolutionary response occurred when the density dependence in growth was switched off entirely.

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For the final component of our robustness analysis, we tested the effect of changing the assumed genetic coefficient of variance CV_G in the initial population on evolution of the PMRN: as expected, increasing CV_G between 0 and 12% accelerated the evolutionary reduction of the PMRN intercept (Figure A1d).

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Table A1. Detailed results of the robustness analysis. Results shown are the mean genetic trait values after 100 years of fishing with a harvest probability of 0.5 and a minimum size limit of 60 cm. Intercept and slope are the probabilistic maturation reaction norm (PMRN) intercept and slope, respectively. GSI is the gonado-somatic index.

Parameter name and value capacity	Intercept (cm)	Slope (cm yr^{-1})	GSI	Growth (cm)
Maximum length increment g_{max}				
40 cm	57.9	−0.0525	0.130	6.00
50 cm	60.2	−0.0518	0.131	7.69
60 cm	62.0	−0.0524	0.131	9.37
70 cm	64.5	−0.0523	0.124	11.0
80 cm	67.3	−0.0520	0.126	12.3
90 cm	71.1	−0.0519	0.124	13.4
100 cm	73.8	−0.0518	0.121	14.4
Density-dependent mortality constant s_0				
$1.0 \cdot 10^3$	70.9	−0.0520	0.125	12.8
$2.0 \cdot 10^3$	69.1	−0.0520	0.126	12.5
$3.0 \cdot 10^3$	68.9	−0.0522	0.126	12.5
$4.0 \cdot 10^3$	67.9	−0.0522	0.126	12.4
$5.0 \cdot 10^3$	67.8	−0.0521	0.126	12.3
$6.0 \cdot 10^3$	67.2	−0.0523	0.126	12.3
$7.0 \cdot 10^3$	67.1	−0.0519	0.126	12.3
$8.0 \cdot 10^3$	66.8	−0.0520	0.126	12.2

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$9.0 \cdot 10^3$	66.6	−0.0519	0.127	12.3
$10.0 \cdot 10^3$	66.6	−0.0520	0.127	12.2

Density-dependent growth constant c_{11}

$0\ 10^{-8}\ g^{-1}$	79.4	−0.0522	0.121	14.1
$0.01\ 10^{-8}\ g^{-1}$	75.2	−0.0517	0.123	13.5
$0.1\ 10^{-8}\ g^{-1}$	71.8	−0.0519	0.125	13.0
$0.4\ 10^{-8}\ g^{-1}$	69.3	−0.0519	0.125	12.7
$1.0\ 10^{-8}\ g^{-1}$	67.3	−0.0520	0.126	12.3
$2.1\ 10^{-8}\ g^{-1}$	66.3	−0.0521	0.126	12.1
$3.4\ 10^{-8}\ g^{-1}$	65.7	−0.0522	0.127	12.0
$6.6\ 10^{-8}\ g^{-1}$	65.1	−0.0521	0.127	11.9
$10.2\ 10^{-8}\ g^{-1}$	64.5	−0.0520	0.126	11.8
$15.2\ 10^{-8}\ g^{-1}$	64.3	−0.0522	0.127	11.8
$21.5\ 10^{-8}\ g^{-1}$	64.4	−0.0522	0.126	11.8

Genetic coefficient of variation CV_G in the initial population

0 %	93.0	−0.0520	0.118	12.8
1 %	92.4	−0.0520	0.119	12.8
2 %	90.7	−0.0520	0.119	12.9
3 %	88.0	−0.0519	0.120	12.8
4 %	84.1	−0.0520	0.120	12.8
5 %	80.0	−0.0520	0.121	12.8
6 %	75.3	−0.0520	0.123	12.7
7 %	71.2	−0.0520	0.124	12.5
8 %	67.3	−0.0520	0.126	12.3

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9 %	64.8	−0.0522	0.128	12.1
10 %	61.7	−0.0523	0.131	12.0
11 %	60.4	−0.0517	0.134	11.7
12 %	59.0	−0.0519	0.136	11.6

9 %   64.8   −0.0522   0.128   12.1

Figure Caption for Appendix 1

Figure A1. Robustness analysis for the eco-genetic model of Atlantic cod. Panels show the (a) genetic growth capacity and the (b-d) probabilistic maturation reaction norm (PMRN) intercept after 100 years of harvesting. Parameters varied are the (a) maximal length increment g_{max} (Equation 2d), the (b) density-dependent mortality constant s_0 (Equation 3a), the (c) density-dependent growth constant c_{11} (Equation 3f), and the (d) genetic coefficient of variation CV_G in the initial population. Harvest probability was 0.5, minimum length limit was 60 cm, and results show the means and standard deviations for 30 independent model runs. Triangles indicate the default parameter values from Table 2 and error bars show the standard deviations.

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Figure A1.