A deterministic eco-genetic model for the short-term evolution of exploited fish stocks

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ABSTRACT

Eco-genetic models describe the contemporary evolution of quantitative genetic traits by integrating the key ecological aspects with the modes of inheritance. Because of the flexibility in incorporating physiological, ecological, and genetic detail, eco-genetic models are typically individual-based and stochastic. Here we propose a deterministic eco-genetic population model to study the evolution of maturation schedules in exploited fish stocks. It is the first deterministic model addressing the evolution of the *probabilistic maturation reaction norm* (PMRN)—the genetic trait recognized to control maturation in fish species. The PMRN is the probability of interseasonal maturation as a function of age and size of juvenile individuals. Being independent of the growth trajectory followed by the individual, it can be considered a non-plastic phenotype, under limited change in temperature and climate. We consider the continuous age and size structures of the fish stock and explicitly represent foraging on a single food resource and mating under 1:1 sex ratio. Inheritance follows a single-locus-two-alleles Mendelian rule to limit the number of genotypes. We adapt the standard escalator boxcar train method for the simulation of physiologically structured population models to the case of two-dimensional age distributions—mature individuals being also distributed according to the age at maturation. The model simulations qualitatively reproduce empirical trends, specifically the genotypic redistribution toward early-maturing types under increasing exploitation and the eventual collapse of the stock. Interestingly, increased effort targeted at large sizes seems to erode the genetic diversity, an effect missed by stochastic models that might serve as warning to fishery managers and policy makers.

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1. Introduction

Eco-genetic modeling is a tool introduced by Dunlop et al. (2009b) to study the contemporary evolution of genetic traits with a tight coupling with empirical data. It combines well established building blocks of life-history evolutionary theory that are considered necessary to obtain realistic predictions. Specifically (see Dunlop et al., 2009b, for more detail):

1. *Process-based description of demographic mechanisms*, to allow a mechanistic approach to demographic change (Gurney and Nisbet, 1998).
2. *Population structure*, as survival and reproductive success of individuals typically depend on age, size, maturation status, and phenotypes (Metz and Diekmann, 1986).
3. *Density and frequency dependences*, as individual development and reproduction are significantly affected by the absolute and relative abundances of the different phenotypes composing the population, primarily because the presence of conspecifics alters food and mates availabilities (Bromley, 1989; Post et al., 1999). In turn, individual sizes shape many life-history traits (Lorenzen and Enberg, 2002) and ultimately fitness (Metz et al., 1992), thus closing the ecological feedback.
4. *Phenotypic plasticity*, to disentangle the environmental from the genetic contribution to individual phenotypes (Scheiner, 1993).

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5. *Genetic variation*, to explicitly model adaptive evolutionary change in the short-term demographic time scale (Houle, 1992). Genetic mutations can be included, though eco-genetic models typically work over decades or centuries and are unsuited for long-term predictions.
6. *Trade-offs*, as typically observed among different components of fitness, such as growth vs survival and somatic growth vs reproductive investment (Stearns, 1992).

Although all previous modeling approaches to life-history evolution—from optimization models (Smith, 1978; Law, 1979) and quantitative genetics (Gomulkiewicz and Kirkpatrick, 1992; Falconer and Mackay, 1996) to adaptive dynamics (Dieckmann and Law, 1996; Geritz et al., 1997, 1998)—incorporate, to some extent, both ecological and evolutionary processes, here by "eco-genetic" we refer to the six above features.

Most of the eco-genetic models so far developed are applied to fishery and follow the stochastic individual-based paradigm (Dunlop et al., 2007, 2009a; Thériault et al., 2008; Enberg et al., 2009), with one deterministic population-based exception (de Roos et al., 2006).

The application to fishery is motivated by the relevant implications—biological, as well as economic and social—of the commercial and recreational practices and by the rapid evolutionary trends observed in the exploited fish stocks. Specifically, the trend toward earlier maturation at smaller sizes has been recognized (see, e.g., Grift et al., 2003; Barot et al., 2004b; Olsen et al., 2004, 2005; Dunlop et al., 2005; Mollet et al., 2007; Jørgensen et al., 2007, Tab. S2 in particular and the refs. therein). This trend has been accompanied by a drop in stock abundance (Hutchings and Reynolds, 2004), in average adult body size (as energy is partly allocated to reproduction after maturation; Hutchings and Reynolds, 2004), in annual growth rate (Swain et al., 2007), and in genetic diversity (Jones et al., 2001); and in some cases the trend ended up with the stock collapse (Hutchings, 2000; Jackson et al., 2001; Bellwood et al., 2004; Hutchings and Reynolds, 2004; Scheffer et al., 2005; Olsen et al., 2005). The evolution toward earlier maturation at smaller sizes is hence to be considered a serious warning for both economic yield and conservation (Jørgensen et al., 2007).

The reason for the typical use of stochastic individual-based models is twofold. The stochastic individual-based paradigm offers ease and flexibility in incorporating all relevant details of the populations' state, processes, and interactions at the individual level (Grimm and Railsback, 2005). Moreover, stochasticity—both at the individual genetic and micro-environmental levels and at the level of the population macro-environment—is listed in Dunlop et al. (2009b) as the seventh important feature, together with points 1–6 above, to obtain quantitative predictions. If fitted on available data sets, it can avoid the explicit modeling of the detailed mechanisms underlying the variability. On the contrary, in a deterministic eco-genetic formulation, explicit modeling is limited by our knowledge about the processes and by the resulting model complexity, so that predictions are typically qualitative.

Specifically for fish populations, the genetic trait regulating maturation is the so-called *probabilistic maturation reaction norm* (PMRN; see Heino et al., 2002; van Dooren et al., 2005; Dieckmann and Heino, 2007). It is defined as the probability of maturation from one reproductive season to the next as a function of actual age and size of immature (juvenile) individuals, and sampling methods for its empirical estimation have been developed (Barot et al., 2004a). The PMRN is by construction independent of the growth trajectory followed by the individual, from birth to actual age and size, and, as such, it is not affected by the environmental conditions on growth. Provided most of the environmental effect on maturation is channeled through growth—i.e., assuming limited change in temperature and climate (Angilletta, 2009; Neuheimer and Grønkjær, 2012)—the PMRN can be considered a non-plastic phenotype, fully determined genetically. In contrast, age and size at maturation are highly plastic phenotypes, since fish that grow fast in low-density and rich environments reach maturity earlier and bigger than fish slow-growing in crowded or poor environments (Bernardo, 1993). Thus, modeling the PMRN as a genetic trait allows to disentangle the genetic from the environmental contribution to age and size at maturation, as their plasticity is indirectly accounted by the growth trajectory of juveniles.

The aim of this paper is to present the first deterministic eco-genetic population model for the short-term evolution of the PMRN of an exploited fish stock. The model could be considered the deterministic version (to some extent) of the fishery model developed in Dunlop et al. (2007) (in the case with no parental care), where the evolution of the PMRN is addressed with a stochastic individual-based approach. With respect to the deterministic model in de Roos et al. (2006), we model maturation as a probabilistic process depending on the age and size of juvenile individuals—the PMRN—whereas a deterministic maturation size (independently of age) is there assumed.

Our motivation for a deterministic description of the PMRN evolution is in line with the tradition of theoretical ecology (Gurney and Nisbet, 1998). Deterministic population models give more compact mathematical descriptions than the stochastic individual-based counterparts. By sacrificing some detail on the underlying populations and processes, deterministic population models typically allow a deeper analysis and a clearer cause–effect relation between processes and results. Most of the times, the analysis is done numerically in both cases, but unraveling general results from many stochastic runs is obviously more problematic. Moreover, beyond simulations, the numerical tools of nonlinear dynamics for the continuation of solutions w.r.t. the many uncertain parameters (Allgower and Georg, 1990; Kuznetsov, 2004; Meijer et al., 2009) make the model's sensitivity analysis very effective. The results, in terms of cause–effect identifications and predictions, have however qualitative nature and therefore corroborates the more quantitative insight obtained with stochastic individual-based models.

Our model works in continuous-time and takes the above features 1–6 into account in a way that is new in the context of deterministic population modeling. The continuous age and size distributions of juvenile and mature individuals are both considered, with mature individuals being also distributed according to the age at maturation, as same-age fish might have reached maturity at different times and growth is traded-off with reproduction after maturation.

In the continuous-time setting, the PMRN is the instantaneous rate of maturation at given age and size (the probability of maturation in the next infinitesimal time interval). We model it as an increasing function of both age and size. The contour line where the PMRN attains half of the frequency of the reproductive season plays the role of the PMRN *midpoint*—the line on which the probability of maturating within the next interseasonal period is 50%. The PMRN midpoint has been often used to picture the PMRN in the age–length plane. The evolutionary trend toward earlier maturation at smaller size is therefore pictured—in both empirical data and models (see, e.g., Olsen et al., 2004; Dunlop et al., 2007)—as a drop of the average PMRN midpoint in the fish stock.

Sexual reproduction is modeled by mating encounters between pairs of asexual individuals (assuming 1 : 1 sex ratio) and the genetic trait of the offspring is determined by a simple genetic model, one-locus-two-alleles with additive effect and no dominance. This gives only three genotypes, mapped into three positions—low, medium, high—of the PMRN midpoint. Human exploitation is described, as in