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How does stochasticity affect evolutionary regime shifts in age and size at maturation?

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Abstract

Fish in many exploited stocks grow faster and mature earlier at either larger or smaller sizes in comparison to pre-exploitation periods. These changes can be driven by both genetic and phenotypic responses. We have shown recently that their interplay can lead to irreversible evolutionary regime shifts in individual life histories and stock properties. Our results were based on a model which assumed annual spawning and size- and density-dependent individual growth in a deterministic environment. We now extend the analysis to cover stochasticity in recruitment, survival after recruitment and harvesting pressure, including the possibility of bycatch and illegal fishing after fishing moratoria or reduced harvest rates are imposed. We show that under low and moderate stochasticity, early maturation at small sizes and late maturation at large sizes can still persist as alternative, evolutionary and ecologically stable states under otherwise identical environmental conditions. Typically, maturation sizes of the late-maturing phenotypes decrease with increasing stochasticity, while those of the early-maturing phenotypes remain nearly constant. Consequently, we confirm that even in stochastic environments, exploitation of late-maturing populations can induce rapid evolution to smaller maturation sizes associated with stepwise decreases in mean age at first reproduction. These changes can be reversed by fishing moratoria; more stochastic environments and/or harvesting pressure require faster closure of the fishery. Unless stochasticity is too strong, incomplete closure of the fishery may also lead to the counterintuitive, accelerated evolution towards smaller sizes at maturation which we reported for the deterministic system.

Introduction

Fish in many exploited stocks exhibit faster growth and mature earlier. These phenotypic life history changes are considered to result from both genetic and plastic responses (Law 2000, Hutchings 2005). The most common plastic response is due to ecological feedback: decreased competition allows for compensatory growth and thus earlier maturation if it occurs around a fixed threshold size (Policansky 1993, Engelhard and Heino 2004). Experimental laboratory studies begin to reveal evolutionary effects of size-selective mortality on an array of individual life history traits and population characteristics (Reznick et al. 1990, Conover and Munch 2002, Munch et al. 2006). Moreover, statistical analyses of data from commercial landings and scientific surveys indicate that such fisheries-induced life history evolution can occur at contemporary timescales (e.g. in cod, Olsen et al. 2004).

Life-history theory predicts that size-specific or indiscriminate harvesting selects for early maturation at small size (Roff 2002, Ernande et al. 2004). We have shown recently that the evolutionary changes can easily become irreversible if the fish exhibit alternative, evolutionary and ecologically stable life histories with early and late maturation (de Roos et al. 2006). Moreover, we have shown that early and complete fishing moratoria are needed to slowly reverse the evolutionary changes, while late or incomplete closures may further aggravate the ongoing evolutionary trend towards early maturation. We used a cohort-based fish stock-resource model in which the growth of individual fish is size- and density-dependent and recruitment is seasonal.

Our model was entirely deterministic and did not incorporate any stochasticity in environmental conditions and individual growth trajectories. We concluded that stochasticity should not change our main results, and referred to a closely related study which examined the impact of stochasticity on population dynamics (van Kooten et al. 2004). Here we extend our previous conclusions and examine the effects of stochasticity in recruitment, adult survival and harvesting pressure on the evolutionary dynamics.

Methods

We use a well-studied size-structured population dynamical model to describe the population dynamics of the fish stock (Persson et al. 1998, de Roos and Persson 2001). The equations

and parameter values describing the individual life history are based on a well-studied, freshwater planktivorous fish (Tables 1 and 2). The population-level equations were summarized in de Roos et al. (2006). The model assumes seasonality in reproduction but no external seasonal input (e.g. fluctuations in temperature). New cohorts recruit to the juvenile and adult population at age 1 and the length of 50 mm with maximum juvenile condition. Young-of-the-year fish do not feed on the common resource, which follows a semi-chemostat dynamics and is shared by all fish older than 1 year. We assume that the number of recruits follows a Ricker-type stock-recruitment relationship corrected for the spawning stock condition, being equal to $R_A E \exp(-2 \cdot 10^{-9} E)$, where E is the total number of eggs spawned the year before recruitment and R_A is the survival probability to age 1 when few eggs are spawned.

We have shown that for parameter values used here, two alternative life histories are both ecologically and evolutionary stable (de Roos et al. 2006). They represent an 'early' phenotype which, in the absence of stochasticity, matures during the second year at only 69 mm length, and a 'late' phenotype which matures only during the third year at 104 mm. The relative advantage of the 'late' phenotype is given by its longer period of juvenile growth, which leads to consistently larger body sizes at any given age and consequently higher reproductive output at each reproductive event. We also assume that maturation at large size yields a relative advantage in feeding ability due to positive correlation between L_{mat} and maximum feeding rate A_{max}. This assumption embodies a mechanism which can oppose selection pressures towards maturation at small size; see Munch et al. (2006) hint at other possible correlations. Both phenotypes are evolutionary stable because they optimize the within-season timing of the onset of maturation (Kozlowski 1996). Unharvested populations of both early- and late-maturing phenotype settle in ecological equilibrium with only minor fluctuations in resource dynamics and fish stock size within seasons (in the absence of stochasticity). We follow this setting here as well.

To examine evolutionary consequences of harvesting in stochastic environment, we use the quantitative genetics approach developed in de Roos et al. (2006). To represent genetic variability in the consumer population, individuals born within the same year are assumed to group into a number of different subcohorts, which are identical at birth, but differ in maturation size L_{mat}. Consumers within the same sub-cohort are assumed to be identical. We use 11 such subcohorts, each with its own phenotype: one with the new mean $L_{mat}^{\star}$ value, five with lower and

five with higher L_{mat} values, equidistantly separated by a factor of $L_{mat}^{\star}\sigma_p/2$ with $\sigma_p = 0.10$. Newborn individuals are distributed over the subcohorts to reflect a discrete approximation to the normal distribution. Selection differential S is calculated using standard techniques, equating individual fitness with the number of eggs spawned; in each reproductive event, S equals the difference between the mean L_{mat} weighed by cohort fecundity and mean L_{mat} in all 1+ year old fish. We constrain the change in L_{mat} between the parent and offspring generation as $\Delta(L_{mat}) = \min(h^2 S, L_{mat}^{\star}\sigma_p/2)$ to keep the phenotypic distribution approximately normal, and assume constant heritability $h^2 = 0.3$.

We model harvesting mortality as in de Roos et al. (2006). Probability of being harvested increases sigmoidally with body size and is characterized by the harvesting size threshold T (measured in mm), at which harvesting reaches half its maximum value, and the harvesting intensity h_{max}, i.e. the annual harvesting mortality for individuals well above the threshold. We harvest a fraction $h_{max}/(1 + \exp(0.15(T - l)))$ of each size class l (measured in mm) of recruited fishes each year prior to reproduction and recruitment.

We incorporate three different sources of environmental stochasticity directly into the model. First, we assume that recruitment is random with $R_A \sim N(0.01, \sigma_{recr}^2)$ and examine a low and high level of stochasticity with $\sigma_{recr}^2 = 0.001$ and 0.006, respectively. Second, we assume that survival of the recruited fish is stochastic. For the sake of computational simplicity, we assume that the background mortality rate $\mu_b \sim LogN(\log(0.014), \sigma_\mu^2)$ is constant within each year, and consider low and high level of stochasticity given by $\sigma_\mu^2 = 0.02$ and 0.15, respectively. Third, we assume that harvesting intensity is random after the onset of harvesting: $h_{max} \sim N(h_{max}^{\star}, \sigma_{harv}^2)$ with a low and high level of stochasticity given by $\sigma_{harv}^2 = 0.025$ and 0.1, respectively. All values below 0 and any large fluctuations beyond four standard deviations are truncated in all stochastic parameters . All values of h_{max} above 0.8 are also truncated to avoid a complete collapse of the stock. On the other hand, we allow for a limited level of by-catch and illegal fishing during a full fishing moratorium by considering $h_{max} \sim N(0, \sigma_{harv}^2)$ with negative values truncated. Finally, we emphasize that the resulting stochasticity in individual survival indirectly feeds back via the resource and thus leads to stochastic growth rates (between age cohorts).

In sum, we consider four levels of stochasticity in the absence of harvesting (low/high in re-

cruitment and low/high in survival of 1+ yr old fish). The resulting annual survival probabilities
are illustrated in Fig. 1.

Results

Impact of stochasticity on age and size at maturation: unharvested populations

In the absence of fishing, the 'early' phenotype is evolutionary stable for all four levels of
stochasticity and the corresponding size at maturation L_{mat} remains approximately constant
or even marginally increases with increasing level of stochasticity. On the contrary, size at
maturation L_{mat} corresponding to the 'late' phenotype decreases from a value close to the fully
deterministic model when both stochasticities are low (A in Fig. 2) to only $\sim$90 mm when
the stochasticity in recruitment is high and stochasticity in 1+ yr old fish is low (C in Fig. 2).
The 'late' phenotype is no longer evolutionary stable when both stochasticities are high (D in
Fig. 2). Despite the stochasticity, fluctuations in L_{mat} over generations remain negligible for
both phenotypes; the increasing variability in age at maturation reflects the increasing variation
in growth rates experienced by different age cohorts.

Impact of stochasticity on age and size at maturation: harvested populations

Possible qualitative evolutionary outcomes of harvesting depend both on the harvesting mortal-
ity and harvesting threshold. We first examine in detail results for the harvesting threshold h_{size}
set at 100 mm and harvesting mortality initially set at 0.6 in average. We have shown earlier
that this harvesting regime induces a rapid evolution of the 'late' phenotype towards the 'early'
phenotype, i.e. towards maturation during the second year at ca. 70 mm length. This trend can
be reversed by complete moratoria imposed no longer than ca. 30 years after the onset of har-
vesting. Here we show that this result holds also for increased levels of stochasticity but the
time span required for successful recovery of the life history characteristics of the 'late' phe-
notype becomes progressively shorter as the stochasticity increases. Figure 3 shows size and

age at maturation (black and grey lines, respectively) for different levels of stochasticity and different time lags at which the full fishing moratorium is implemented. The three data points correspond to age and size at maturation at the onset of harvesting, at the end of the period of intense harvesting, and after 150 years of fishing moratorium.

The changes of age and size at maturation qualitatively follow the results for deterministic dynamics (Fig. 4; compare de Roos et al. (2006)). The onset of harvesting is first followed by the plastic response (step-like decrease in age at maturation) followed by the evolutionary response (gradual but relatively fast decrease in size at maturation). During the moratorium the stock either slowly recovers towards the 'late' phenotype life history with late maturation at large size (Fig. 4A), or continues to decrease towards the 'early' phenotype life history (Fig. 4B). The corresponding mortality components are shown in Fig. 5A and B, respectively.

Finally, we have investigated the consequences of partial fishing moratoria when the harvesting size threshold h_{size} is set lower at 80 mm. We have shown earlier that under these circumstances but in a deterministic environment, the 'early' phenotype evolves towards larger sizes at maturation but only if exploitation is sufficiently strong (de Roos et al. 2006). Consequently, heavy exploitation of the 'late' phenotype can have only limited evolutionary impact; the fish mature one year earlier but the realized decrease in size at maturation is limited and may be easily reversible. Partial moratoria are very detrimental in such cases as they accelerate the evolution towards smaller sizes and the final size can be much smaller and irreversible.

Again, these results hold even if we include stochasticity except when the stochasticity in recruitment is too strong; the 'late' phenotype then evolves towards the same size at maturation irrespective of having full or partial fishing moratorium (Fig. 6).

Discussion

In this study we examined how stochasticity in recruitment, survival of older fish and harvesting affects evolution in age and size at maturation in exploited fish stocks. We showed that our previous results based on a fully deterministic model remain in place as long as the stochasticity is not too strong.

Several additional results emerge from our analysis. For the particular choice of parameters

made above, the 'early' phenotype does not respond evolutionarily to increased stochasticity in survival rates while the 'late' phenotype does. The observed decrease in evolutionary stable size at maturation of the 'late' phenotype is is apparently due to the fact that it has much less 'elbow room' with increased fluctuations in survival, especially if survival becomes very low. Consequently, harvesting-induced changes in the 'late' phenotype become more easily irreversible as stochasticity increases. Among all possible causes, the following one is obvious and trivial: since the size of the 'late' phenotype decreases with stochasticity, the time before it reaches the size limit of irreversibility becomes shorter. However, a reverse result is also possible: the pure 'early' phenotype can disappear at moderate levels of stochasticity and the only remaining phenotype is much closer to the 'late' phenotype (Boukal et al., other parameter values, unpublished data).

The evolutionary process during the fishing moratorium can be unpredictable (e.g. Fig. 3A, $\sigma_{harv}^2 = 0.1$) and either result in slow recovery of life history traits or fail to do so. Statistical analysis of maturation data for cod (*Gadus morhua*) in the Northwest Atlantic also shows predominately slow rate of evolutionary recovery during the moratorium (Olsen et al. 2004). It cannot be excluded that the stocks actually hover around or just above the limit which still allows for successful evolutionary recovery. If this is true, the 1992 moratorium on cod fishing imposed by the Canadian government has been implemented in the very last moment.

Current developments, such as the individual-based eco-genetic models, begin to tease apart the most important mechanisms responsible for fisheries-induced evolution in a stochastic world. However, the history of similar approaches is modest at best. So far, only few published studies have examined the role of stochasticity in harvesting-induced life history evolution. Martinez-Garmendia (1998) concluded that evolutionary responses, which should be small even in a deterministic setting, should be further weakened by stochasticity in recruitment. Unfortunately, the individual-based modelling framework used in that study is very difficult to interpret. An age-structured model of an exploited fish stock by Heino (1998) is close to our approach as it included stochasticity in recruitment and stock estimate (analogous to stochasticity in harvest rate in our model). However, due to the age-based approach, it could properly disentangle the role of phenotypic plasticity. Finally, Tenhumberg et al. (2004) used an inherently stochastic, individual-based model to show that size-selective harvesting can result in much smaller indi-

viduals when the entire population is harvested. However, their model also did not allow for plastic responses and, above all, studied kangaroos.

Our modelling approach, based on a detailed description of individual life history processes, has the advantage of simultaneously covering both evolutionary and plastic repsonses. It suggests that stochasticity may have only limited impact on fisheries-induced evolution in exploited fish stocks. Deterministic models can thus provide valuable insight into evolutionary processes in marine organisms, although the environment in which they live is inherently stochastic.

Acknowledgements

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subject	symbol	value	unit	interpretation
Consumer	N	-	#	cohort size
	x	-	g	irreversible mass
	y	-	g	reversible mass
Growth season	Y	90	day	length of year
Resource	R	-	g L^{-1}	resource density
	r	0.1	d^{-1}	population growth rate
	K	0.003	g L^{-1}	carrying capacity
	V	10^9	L	lake volume
Ontogeny	w_b	1.4×10^{-3}	g	total egg mass
	l_{exp}	0.29	-	allometric exponent
	l_c	50.2	mm g$^{-l_{exp}}$	allometric scalar
	L_{mat}	varied	mm	maturation size (body length)
	q_j	0.74	-	juvenile max. condition
	q_a	1.0	-	adult max. condition
	k_r	0.5	-	gonad-egg conversion efficiency
Planktivory	α	1.0	-	allometric exponent
	A_{max}	1.0×10^5	L d^{-1}	max attack rate
	w_o	50.0	g	optimal foraging size (standardized mass)
Handling	ξ_1	6.0	d g$^{-(1+\xi_2)}$	allometric scalar
	ξ_2	-0.81	-	allometric exponent
Metabolism	ρ_1	0.033	g$^{(1-\rho_2)}$d^{-1}	allometric scalar
	ρ_2	0.77	-	allometric exponent
	k_e	0.61	-	conversion coefficient
Mortality	μ_0	0.014	d^{-1}	background mortality rate
	q_s	0.2	-	starvation condition threshold
	s	0.2	d^{-1}	starvation rate coefficient

Table 1: Variables and model parameters. All parameters except Y, R, r, K and V refer to individual-level processes. All values based on a well-studied freshwater system involving a planktivorous fish and zooplankton (de Roos and Persson, 2001).

Subject	Equation
Standardized mass	$w(x) = (1 + q_j)x$
Body length	$L(x) = l_c(w(x))^{l_{exp}}$
Attack rate	$A(x) = A_{max}\left(\frac{w(x)}{w_o}\, e^{\left(1 - \frac{w(x)}{w_o}\right)}\right)^{\alpha}$
Handling time	$H(x) = \xi_1\, w(x)^{\xi_2}$
Food intake rate	$I(x) = \dfrac{A(x)R}{1 + H(x)A(x)R}$
Assimilated energy	$E_a(x) = k_e I(x)$
Maintenance requirements	$E_m(x, y) = \rho_1(x + y)^{\rho_2}$
Energy balance	$E_g(x, y) = E_a(x) - E_m(x, y)$
Fraction of energy allocated to growth in irreversible mass	$\kappa(x, y) = \begin{cases} \dfrac{y}{(1 + q_j)q_j x} & \text{if } L(x) \leq L_{mat} \text{ and } E_g > 0 \\[2ex] \dfrac{y}{(1 + q_a)q_a x} & \text{if } L(x) > L_{mat} \text{ and } E_g > 0 \\[2ex] 0 & \text{otherwise} \end{cases}$
Starvation mortality	$\mu_s(x, y) = \begin{cases} s\left(q_s \dfrac{x}{y} - 1\right) & \text{if } y < q_s x \\[2ex] 0 & \text{otherwise} \end{cases}$
Total mortality	$\mu(x, y) = \mu_0 + \mu_s(x, y)$
Fecundity	$F(x, y) = \begin{cases} k_r\,(y - q_j x)/w_b & \text{if } L(x) > L_{mat} \text{ and } y > q_j x \\ 0 & \text{otherwise} \end{cases}$

Table 2: Individual-level equations used in the simulations, see also de Roos and Persson (2001) and de Roos *et al.* (2006).
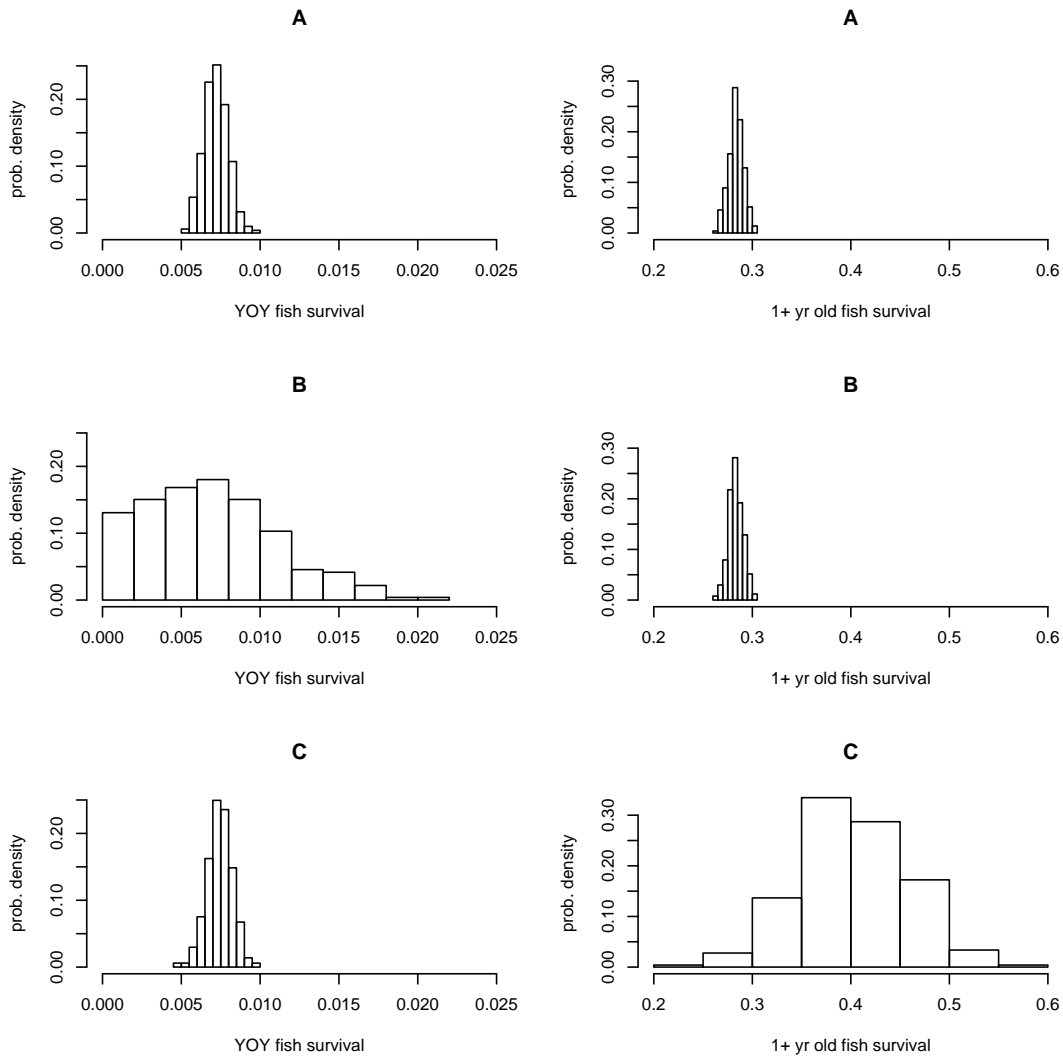
Figure 1: Histograms of YOY fish (left column) and 1+ yr old fish (right column) for different levels of stochasticity. **A.** Low stochasticity in recruitment ($\sigma^2_{recr} = 0.001$) and survival of recruited fish ($\sigma^2_{\mu} = 0.02$). **B.** High stochasticity in recruitment ($\sigma^2_{recr} = 0.006$) and low stochasticity in survival of recruited fish ($\sigma^2_{\mu} = 0.02$). Recruitment may entirely fail in some years. **C.** Low stochasticity in recruitment ($\sigma^2_{recr} = 0.001$) and high stochasticity in survival of recruited fish ($\sigma^2_{\mu} = 0.15$). All results based on data from 100 years in five simulation replicates and shown as mean $\pm$ 1 SD.
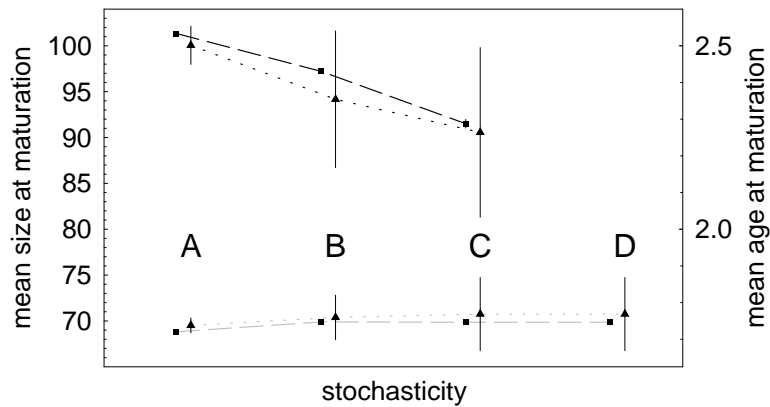
Figure 2: The response of evolutionary and ecologically stable 'early' phenotype (grey lines) and 'late' phenotype (black lines). Size at maturation = squares and dashed lines; age at maturation = triangles and dotted lines. **A.** Low stochasticity in recruitment ($\sigma^2_{recr} = 0.001$) and survival of recruited fish ($\sigma^2_{\mu} = 0.02$). **B.** High stochasticity in recruitment ($\sigma^2_{recr} = 0.006$) and low stochasticity in survival of recruited fish ($\sigma^2_{\mu} = 0.02$). Recruitment may entirely fail in some years. **C.** Low stochasticity in recruitment ($\sigma^2_{recr} = 0.001$) and high stochasticity in survival of recruited fish ($\sigma^2_{\mu} = 0.15$). **D.** High stochasticity in recruitment ($\sigma^2_{recr} = 0.006$) and high stochasticity in survival of recruited fish ($\sigma^2_{\mu} = 0.15$). All results based on data from 100 years in five simulation replicates and shown as mean $\pm$ 1 SD.
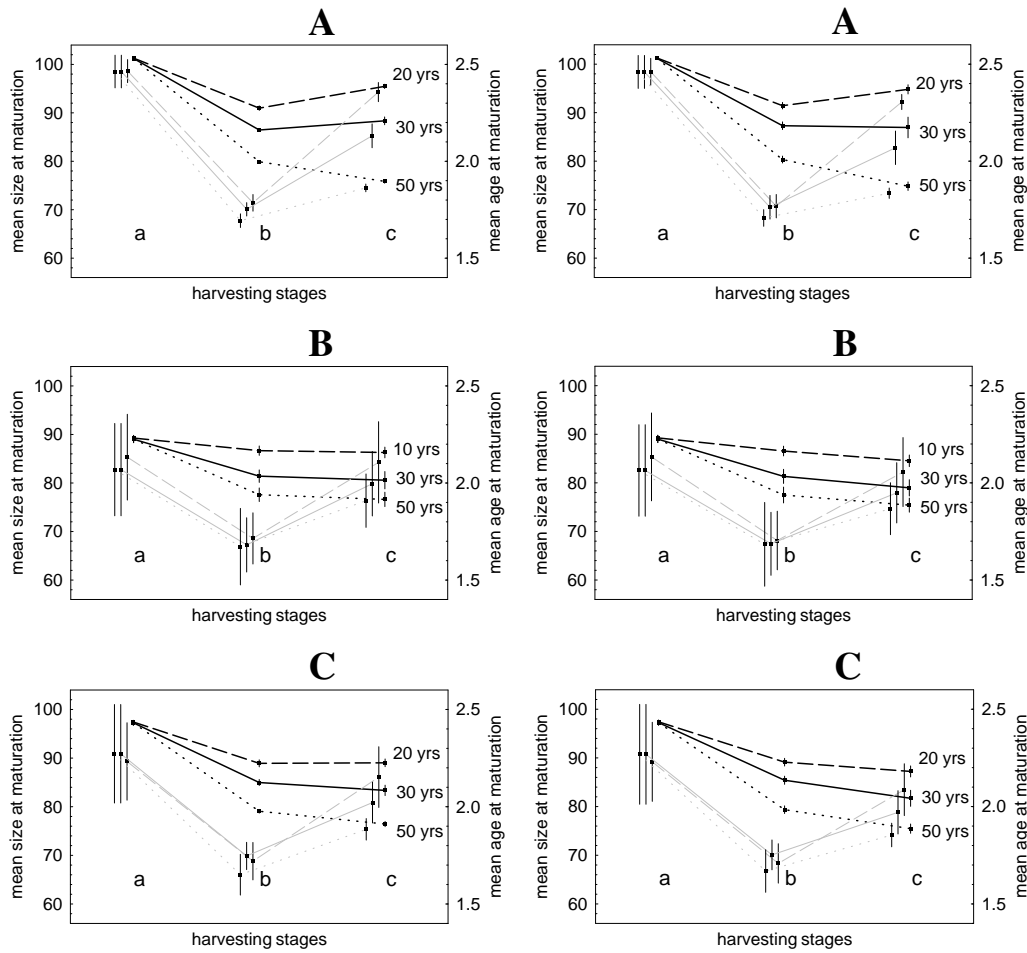
Figure 3: Fisheries-induced evolution of the 'late' phenotype for different levels of stochasticity. **A.** Low stochasticity in recruitment and survival of recruited fish ($\sigma_\mu = 0.02, \sigma_{recr} = 0.001$). **B.** High stochasticity in recruitment and low stochasticity in survival of recruited fish ($\sigma_\mu = 0.02, \sigma_{recr} = 0.006$). Recruitment may entirely fail in some years. **C.** Low stochasticity in recruitment and high stochasticity in survival of recruited fish ($\sigma_\mu = 0.15, \sigma_{recr} = 0.001$). Left column: low stochasticity in harvesting ($\sigma_{harv} = 0.025$); right column: high stochasticity in harvesting ($\sigma_{harv} = 0.1$). The consecutive data points (a,b,c) in each panel show age (grey lines) and size (black lines) at maturation before the onset of harvesting, at the end of the intensive harvesting period, and after 150 years of a complete fishing moratorium. Different lines show different periods of harvesting. All data based on 10 simulation replicates and shown as mean $\pm$ 1 SD.
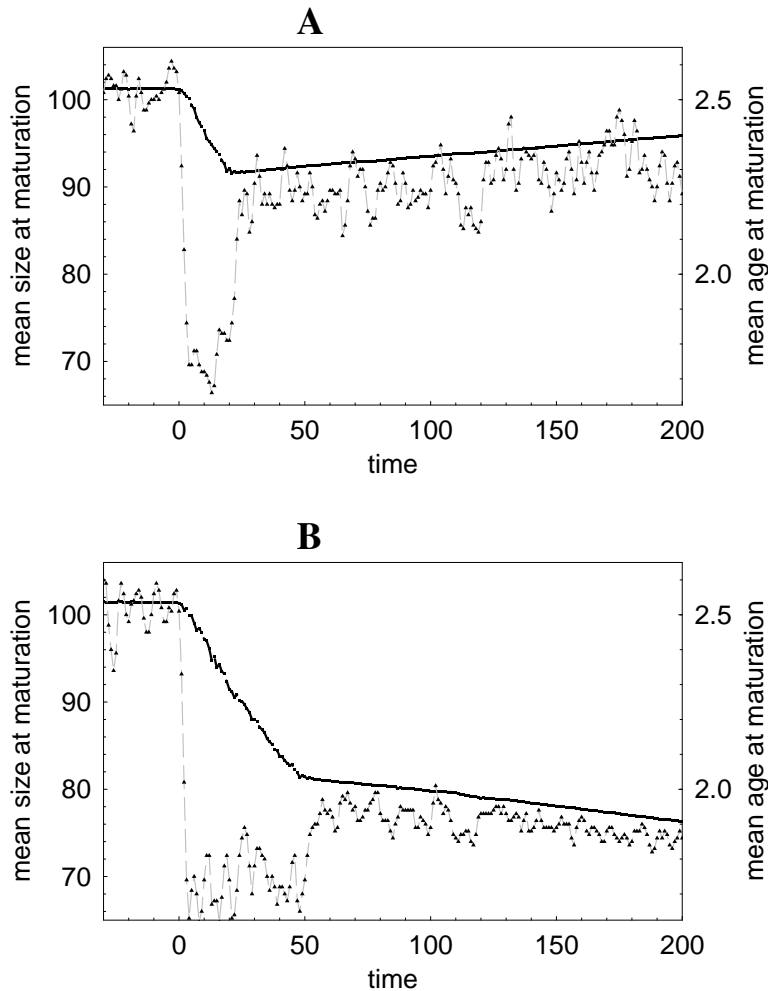
Figure 4: Fisheries-induced evolution of 'late' phenotype: examples of the effect of moratoria on size (black line) and age (grey broken line and triangles) at maturation. Mean harvesting intensity equal to 0.6; high harvesting size threshold ($h_{size} = 100$ mm). Low stochasticity in recruitment, survival of recruited fish as well as harvesting. **A.** Early moratorium after 20 years followed by recovery of age and size at maturation. **B.** Late moratorium after 50 years followed by further decrease in age and size at maturation towards the 'early' phenotype.
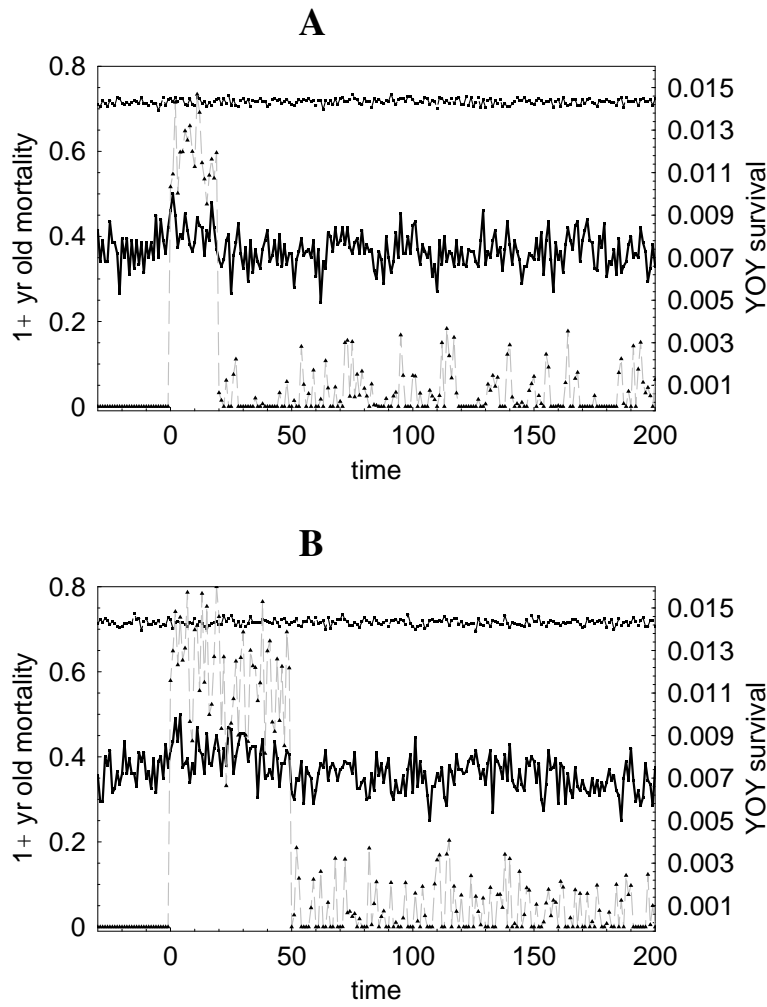
A

B

Figure 5: Harvesting mortality (broken grey line, triangles), natural mortality (broken black line) and survival to age 1 (solid black line) associated with the evolutionary dynamics in Fig. 4A and B.
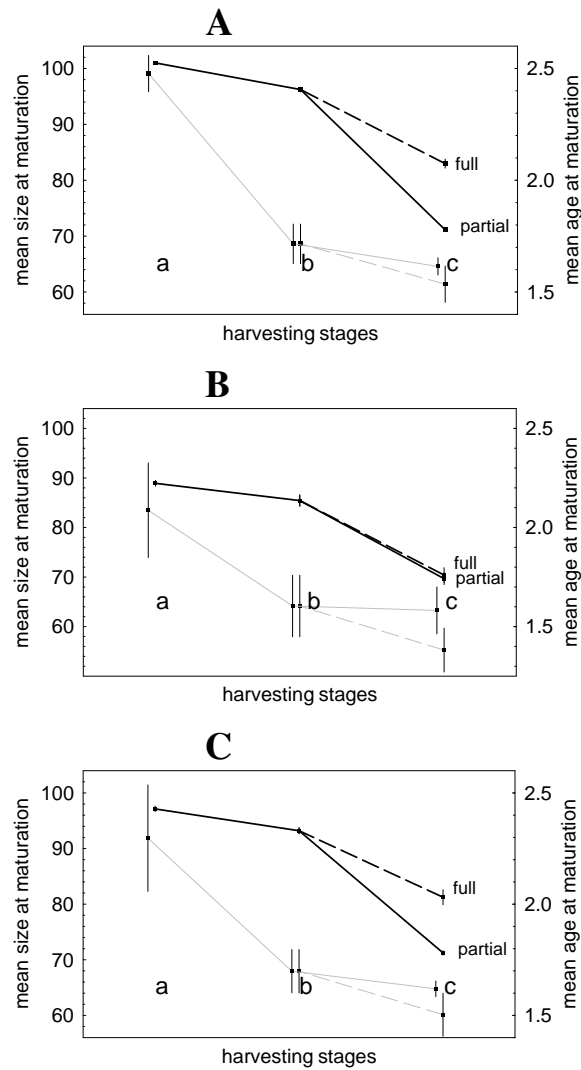
Figure 6: Fisheries-induced evolution of 'late' phenotype: the effect of continued full exploitation ('full', broken line) and partial moratoria ('partial', solid line). Mean harvesting intensity equal to 0.6, kept either constant or reduced to 0.3 during a partial moratorium imposed 30 years after the onset of harvesting. Low harvesting size threshold ($h_{size} = 80$ mm); high stochasticity in harvesting. The consecutive data points (a,b,c) in each panel show age (grey broken lines) and size (black lines) at maturation before the onset of harvesting, after 30 years and after 180 years of fishing. **A.** Low stochasticity in recruitment and survival of recruited fish. **B.** High stochasticity in recruitment and low stochasticity in survival of recruited fish. **C.** Low stochasticity in recruitment and high stochasticity in survival of recruited fish. All data based on 10 simulation replicates and shown as mean $\pm$ 1 SD.