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Ecological and Evolutionary Recovery of Exploited Fish Stocks

Katja Enberg[1], Erin S. Dunlop[1], Mikko Heino[1,2,3] and Ulf Dieckmann[1]

[1] *Evolution and Ecology Program, International Institute for Applied Systems Analysis, A-2361 Laxenburg, Austria*

[2] *Institute of Marine Research, P.O. Box 1870 Nordnes, N-5817 Bergen, Norway*

[3] *Department of Biology, University of Bergen, P.O. Box 7800, N-5020 Bergen, Norway*

**Corresponding author; phone: +43 2236 807 249; e-mail: enberg@iiasa.ac.at*

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Collapses of ecological populations have occurred throughout natural history. Such events may occur due to demographic stochasticity, non-equilibrium population dynamics, or interactions with other species. However, a major cause of collapses is human activity, such as fishing, hunting, or habitat alteration. The depleted state of many fisheries forces the managers to deal with recovery processes of over-exploited and collapsed fish stocks, and thus also the scientists to study the mechanisms and means for successful recoveries.

Evolutionary changes caused by fisheries are known to affect the genetic and phenotypic structure of exploited fish stocks (Grift *et al.* 2003, Olsen *et al.* 2004, 2005, Barot *et al.* 2005). These changes have been most visible in terms of the life-history characteristics influencing age and size at maturation. Most exploitation is selective: it might target for example moose or deer with large or high-quality antlers (Solberg *et al.* 2000, Scribner *at al.* 1989). In fisheries, selection is strongly based on the size of individuals (Myers & Hoenig 1997, Jennings *et al.* 2001). In general, increased exploitation of larger (or older) individuals decreases the size and age at maturation. This, in turn, tends to decrease the reproductive potential of fish populations, as large individuals produce disproportionate more offspring (May 1967, Pinhorn 1984, Kjesbu *et al.* 1998, Marteinsdottir *et al.* 2000), which may lead to lower yields and to a reduction in the recovery potential after a collapse. Importantly, also an increased mortality that is uniformly applied to all individuals of a population favours earlier maturation.

Fisheries-induced changes can be caused by different mechanisms: (1) demographic changes: as larger and older individuals are removed from a stock, the population becomes dominated by small and young fish, (2) phenotypic plasticity: as population biomass decreases, a resultant increase in resource availability may allow individuals to grow faster and thus mature earlier, and (3) genetic changes: size-selective harvesting removes those individuals that would mature late and large without allowing them to reproduce, so that only individuals maturing at earlier ages and smaller sizes will contribute to the next generation's gene pool.

The effects of environmental fluctuations on population dynamics have been studied extensively. Often the impact of such noise is expressed in terms of the probability of extinction of the target species. In general, environmental fluctuations of increasing strength aggravate the extinction risk (Roughgarden 1975, May & Oster 1976, Tuljapurkar 1989, Lande 1993). In contrast to such demographic considerations, the effects of environmental stochasticity on fisheries-induced evolution have been little studied to date. A notable exception is an earlier claim that increased stochasticity in recruitment would preclude fisheries-induced evolution (Martinez-Garmendia 1998).

In our study we use an individual-based eco-genetic model with multiple evolving life-history traits (Dunlop 2005). This modelling framework combines population dynamical and evolutionary processes. The model was parameterized for a cod-like life history. The maturation schedule of individuals is modelled through a linear probabilistic maturation reaction norm (PMRN, Heino *et al.* 2002) and three parameters of this PMRN (namely its slope, intercept, and width) are allowed to evolve in the model. Further evolving traits are reproductive investment (quantified in terms of the gonadosomatic index, GSI) and intrinsic growth rate (which trades off with survival). To identify the effects of evolutionary change on recovery processes – as compared with more traditional models that do not account for fisheries-induced life-history changes – we explored a model population's response to fishing with and without evolution. To quantify the effects of environmental noise on the probability of collapse, on fisheries-induced evolution, and on recovery potential, we included fluctuations in growth and recruitment.

Our preliminary results highlight the importance of accounting for the life-history changes caused by fisheries when trying to understand and predict the recovery of exploited stocks (Figs. 1 and 2).

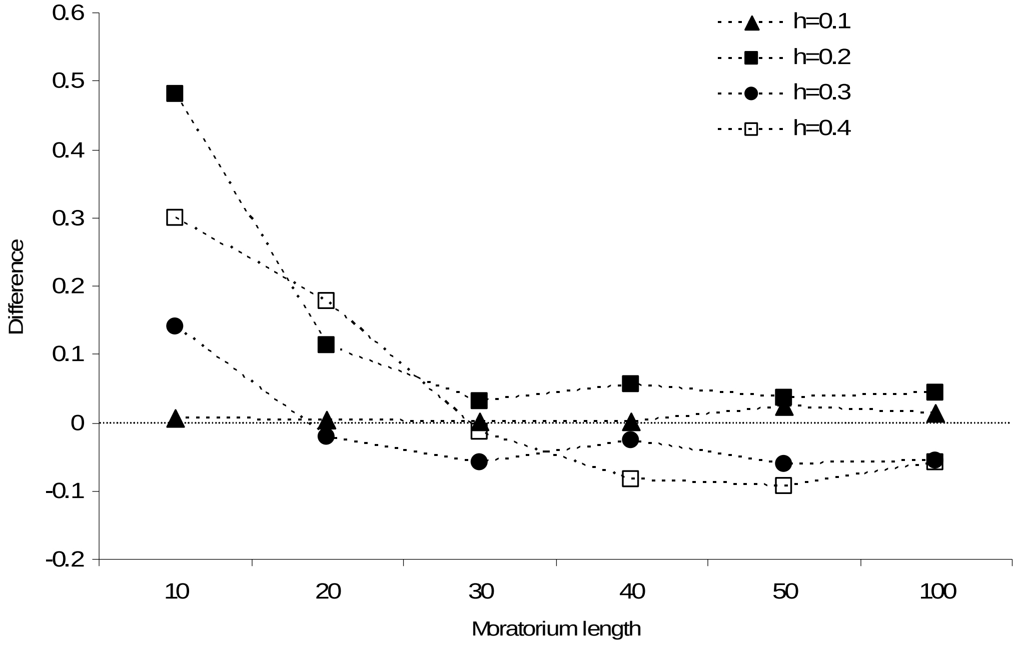

Figure 1. Difference between recovery processes in population abundance including and excluding evolutionary effects. Symbols indicate different constant harvest rates. The difference is calculated from the proportional recovery to the pre-harvesting population size, and positive values indicate better recovery due to fisheries-induced evolutionary changes.

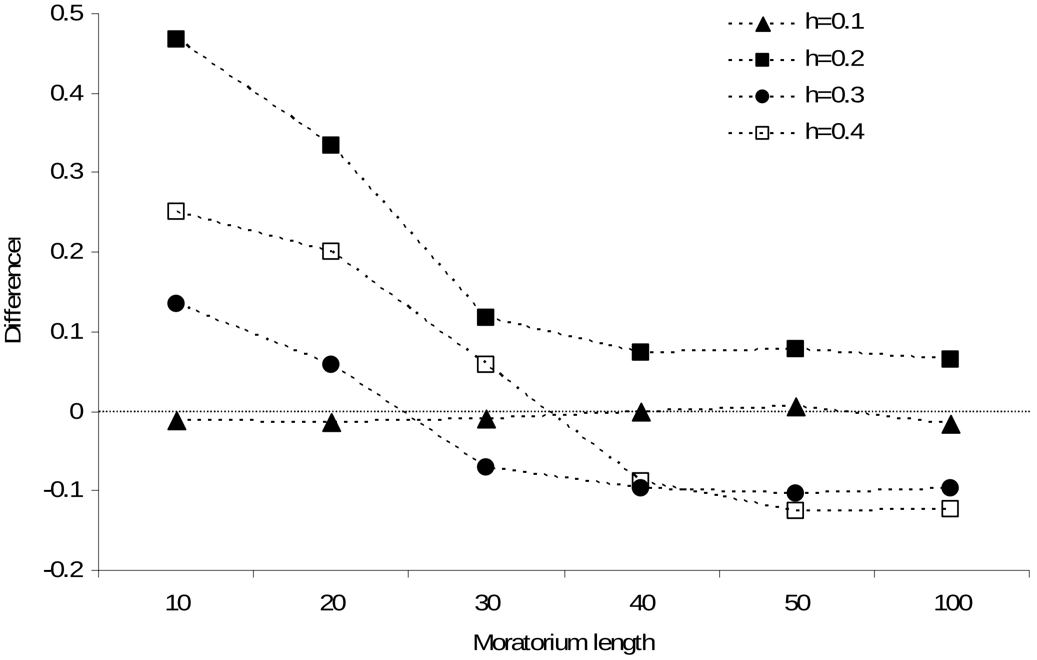

Figure 1. Difference between recovery processes in spawning stock biomass (SSB) including and excluding evolutionary effects. Symbols indicate different constant harvest rates. The difference is calculated from the proportional recovery to the pre-harvesting SSB, and positive values indicate better recovery due to fisheries-induced evolutionary changes.

The impact of fisheries induced evolution is dependent on both the harvest rate and also on the temporal scale on which the success of recovery is judged, that is, on the duration of moratorium. Moreover, we show that, in contrast to earlier suggestions (Garmendia-Martinez 1998), the inclusion of stochastic recruitment variability has only minor effects on the incidence of fisheries-induced evolution.

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