Reaction norms for age and size at maturation in Atlantic cod stocks

Mikko Heino[1,2] & Ulf Dieckmann[2]

1 Institute of Marine Research, Box 1870 Nordnes, N-5817 Bergen, Norway (mikko@imr.no)

2 Adaptive Dynamics Network, International Institute for Applied Systems Analysis (IIASA), A-2361 Laxenburg, Austria (dieckmann@iiasa.ac.at)

This article provides a short overview of research we have carried out in collaboration with fisheries research institutes in Europe and North America to elucidate long-term changes in the maturation reaction norms of Atlantic cod (*Gadus morhua*).

Reaction norms for age and size at maturation, describing the age and size dependence of an organism's maturation process, were first introduced by Stearns and Koella (1986). Maturation is not, however, fully determined by age and size alone. The residual effects not captured by age and size introduce an unavoidable probabilistic element to the description of the maturation process. Taking this probabilistic nature of maturation into account is crucial if maturation reaction norms are to be estimated from data. The probabilistic reaction norm for age and size at maturation (Heino et al. 2002a) is defined as the probability that an immature individual, depending on its age and size, matures during a given time interval. A probabilistic reaction norm is thus specified by determining these probabilities for all relevant ages and sizes (see Figure).

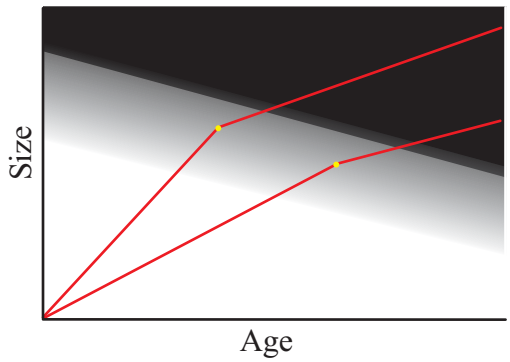

Figure 1. Probabilistic reaction norms for age and size at maturation describe how the probability of an organism maturing during a given time interval depends on its age and size. Shades of grey illustrate how this probability may increase with age and size. Two growth trajectories are shown in red, one for a slow-growing fish and one for a fast-growing fish. Yellow dots indicate the age and size at which these fish mature

The traditional way of describing maturation in fisheries science is based on so-called maturity ogives. These depict the proportions of mature individuals as functions of age and/or size. However, it is crucial to realize that maturity ogives characterize only the maturity status of a stock, and not the maturation process itself. This is because the maturity status of a population is determined not only by the maturation process itself but also growth and survival. When analyzing trends in maturity ogives, changes in the maturation process are thus not distinguishable from changes in the rates of growth and mortality. All three of these factors are affected by fishing, and it is therefore very difficult, if not impossible to use maturity ogives for building an understanding of how specifically exploitation impacts a stock. Maturation reaction norms, by contrast, largely overcome these difficulties: by describing the maturation process itself (in terms of the effects of age and size) they strip away the confounding effects of varying growth and survival. This property of maturation reaction norms facilitates addressing many research problems, including

- Disentangling phenotypically plastic and genetic changes in maturation, and
- Predicting how maturation is influenced by changes in growth and/or mortality.

Both of these tasks are central to assessing, understanding, and predicting the population characteristics of marine organisms. Maturation reaction norms also allow the effects of variations in

factors other than growth and mortality to be studied. This is because many variables, such as food availability and temperature, influence maturation mostly through their effects on growth and survival.

The specific methodology for carrying out estimations of maturation reaction norms for several types of commonly available data is now available (Heino et al. 2002a,b, Barot et al. 2003). While we have so far utilized data from commercially exploited fish stocks, the approach is readily applicable to all sorts of organisms, and even to ontogenetic transitions other than maturation.

Maturation reaction norms have been estimated for six stocks of Atlantic cod (see the Table below). All investigated stocks exhibit clear temporal trends in their maturation reaction norms, always towards increased maturation probabilities at younger ages and smaller sizes, in accordance with predictions from life-history theory. In the Canadian stocks, however, there are signs of a reversal of this trend, resulting from the moratorium declared on fishing in 1992.

Stock	Period with data	Reference
Northeast Arctic	1932-1998	Heino et al. 2002c
Georges Bank	1970-1998	Barot et al. 2003
Gulf of Maine	1970-1998	Barot et al. 2003
Northern	(1977)-1981-2002	Olsen et al., in prep.
Grand Bank	1971-2002	Olsen et al., in prep.
St. Pierre Bank	1972-2002	Olsen et al., in prep.

We have also developed a quantitative genetics model that includes a process-oriented description of fish population dynamics (Dieckmann & Heino, in prep.), based on estimated maturation reaction norms. This model allows predicting the direction and pace of evolutionary changes in maturation reaction norms in response to fisheries-induced selection. In addition, the model can be used to predict the phenotypic and demographic responses of a stock to changes in its environment, e.g., in growth or mortality rates; temperature effects on growth can also be taken into account. A version of this model has been parameterized for Northeast Arctic cod. This model indicates that both the time scale and the magnitude of changes documented in the Northeast Arctic cod's maturation reaction norm are well in accordance with what is expected based on changes in the cod's exploitation regime.

Changes in age and size at maturation are widespread among Atlantic cod stocks (Trippel 1995). Reaction norm analyses suggest that these are caused by fisheries-induced evolutionary changes, in addition to direct demographic and phenotypically plastic effects of fishing. Any long-term analysis on maturation therefore needs to consider that the maturation characteristics of fish stocks are far from being static. Instead, these characteristics vary with environmental conditions, due to phenotypic plasticity, and with exploitation regimes, due to evolutionary changes.

The authors welcome contacts by colleagues interested in collaborating on estimating reactions norms from their data.

Acknowledgements: The authors are indebted to Sébastien Barot, Olav Rune Godø, George Lilly, Loretta O'Brien, and Esben Olsen for collaborations that have been integral to the work reviewed her. Collaborations on this study have been fostered by the European Research Training Network *ModLife*, supported by the Fifth Framework Programme of the European Commission (Contract Number HPRN-CT-2000-00051).

Barot, S., Heino, M., O'Brien, L. & Dieckmann, U. 2002. Reaction norms for age and size at maturation: study of the long-term trend (1970-1998) for Georges Bank and Gulf of Maine cod stocks. ICES CM 2002/Y:3. Also in revision in Ecological Applications.

Barot, S., Heino, M., O'Brien, L. & Dieckmann, U. 2003. Estimating reaction norms for age and size at maturation when age at first reproduction is unknown. IIASA Interim Report. IIASA, Laxenburg. Also in revision in Evolutionary Ecology Research.

Heino, M., Dieckmann, U. & Godø, O. R. 2002a. Measuring probabilistic reaction norms for age and size at maturation. Evolution 56:669-678.

Heino, M., Dieckmann, U. & Godø, O. R. 2002b. Estimation of reaction norms for age and size at maturation with reconstructed immature size distributions: a new technique illustrated by application to Northeast Arctic cod. ICES Journal of Marine Science 59:562-575.

Heino, M., Dieckmann, U. & Godø, O. R. 2002c. Reaction norm analysis of fisheries-induced adaptive change and the case of the Northeast Arctic cod. ICES CM 2002/Y:14.

Stearns, S. C. & Koella, J. C. 1986. The evolution of phenotypic plasticity in life-history traits: predictions of reaction norms for age and size at maturity. Evolution 40:893-913.

Trippel, E. A. 1995. Age at maturity as a stress indicator in fisheries. Bioscience 45:759-771.