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## **Exploitation as a driving force of life history evolution: methods and empirical analyses**

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Today, fishing is the dominant source of mortality in most commercially exploited fish stocks. Life-history theory predicts that, under most circumstances, increased mortality at potential ages and sizes at maturation selects for earlier maturation. Indeed, commercially exploited fish stocks often show trends towards earlier maturation. However, another plausible explanation exists: earlier maturation may simply reflect phenotypic plasticity. Because of this ambiguity in disentangling the plastic and evolutionary components of life history changes, understanding the nature of phenotypic changes in exploited fish populations has been difficult so far. A recently developed new method for estimating probabilistic reaction norms for age and size at maturation is now helping to overcome this problem, and, in most of the cases analysed so far, is suggesting that evolutionary components contribute to the observed trends in age and size at maturation. In this paper we give an overview of the probabilistic reaction norm method and describe the resulting progress with empirical case studies.

Keywords: age and size at maturation, fisheries-induced adaptive change, life history evolution, probabilistic reaction norms

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## 1. Introduction

Concerns about the evolutionary effects of the selective harvesting of fish populations (Rutter 1902) predate the birth of modern fisheries science. Yet it has only been in recently years that this topic started to attract more than sporadic attention (e.g., Law 2000, Browman 2000, Kenchington et al. 2003, Hutchings 2004). Here we briefly review some results on fisheries-induced evolution in maturation tendency, a life-history trait for which recent methodological developments have facilitated the analysis of long time series of life history data collected from some major fish stocks.

## 2. Maturation reaction norms

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 (Figure 1).

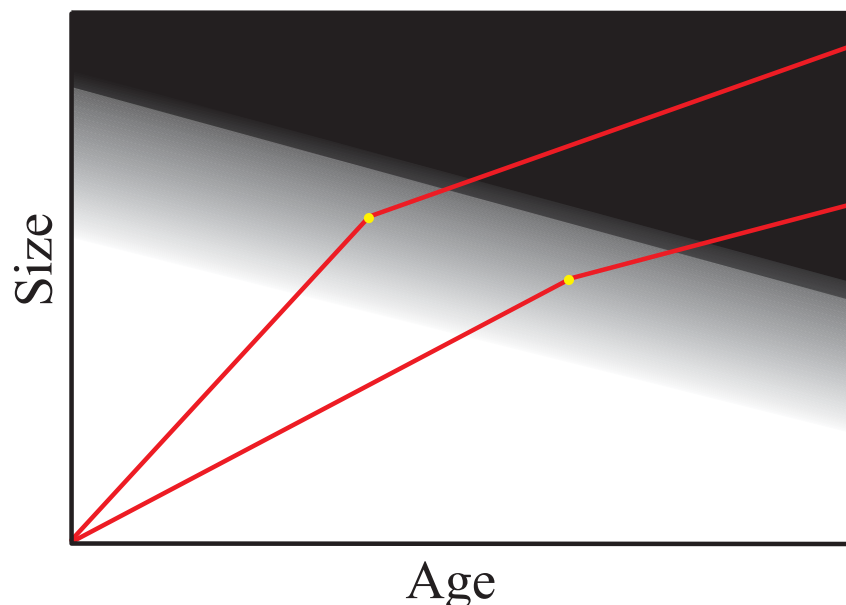


Figure 1. Probabilistic reaction norms for age and size at maturation describe how the probability of an organism maturing during a given time interval depends on its age and size. Shades of grey illustrate how this probability may increase with age and size. Two growth trajectories are shown in red, one for a slow-growing fish and one for a fast-growing fish. Yellow dots indicate the specific combinations of 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 but also by growth and survival. Based on maturity ogives alone, changes in the maturation process are thus indistinguishable from changes in the rates of growth and mortality. Since all three factors are affected by fishing, and it is 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 interesting and practically relevant research problems, including the

- Disentangling of phenotypically plastic and genetic changes in maturation, as well as the
- Prediction of 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.

### ***3. Estimation of maturation reaction norms***

The specific methodology for carrying out estimations of maturation reaction norms for several types of commonly available data is now available. While we have analyzed maturation trends based on data from commercially exploited fish stocks, the approach is readily applicable to all sorts of organisms, and even to ontogenetic transitions other than maturation.

If representative samples of immature and newly matured individuals, sized and aged, were available, estimation of maturation reaction norms would require only a straightforward application of standard statistical methods (Heino et al. 2002a). This conveniently simple situation, however, typically does not apply in practice: for many populations of interest data describing the size and age of either immature or newly matured individuals are missing. The first case may arise when immature and mature parts of the population are spatially segregated. In this case, it is often still possible to estimate the maturation reaction norm through a specific method introduced for reconstructing the missing data (Heino et al. 2002a). The second case arises when the newly matured individuals cannot easily be distinguished from those that

matured earlier. In this case, an alternative estimation method, introduced by Barot et al. (2004a,b), can be applied. Maturation reaction norms can thus be estimated even under some conditions of incomplete stock information.

#### *4. Empirical studies*

Using the new methods mentioned above, maturation reaction norms have been estimated for six stocks of Atlantic cod, for two species of flatfish (representing four stocks), for Norwegian spring-spawning herring (one of world's largest fish stocks), and for one freshwater species, grayling (see Table 1). With the possible exception of Norwegian spring-spawning herring, all investigated stocks exhibit clear temporal trends in their maturation reaction norms: these trends always point towards increased maturation probabilities at younger ages and smaller sizes, in accordance with predictions from life-history theory. In the Canadian cod stocks even signs of a trends reversal could be detected: this reversal is likely to reflect the stocks' response to a moratorium on the directed offshore fishing of cod, declared in 1992.

The case of Norwegian spring-spawning herring is different, as in this stock mostly mature individuals are harvested. Such an exploitation regime is predicted to select for delayed maturation (Law & Grey 1989, Heino 1998, Ernande et al. 2004). Nevertheless, it appears that slow-growing herring nowadays mature at an earlier age than they used to do (Engelhard & Heino 2004). Although confounding factors in the analysis might cause a spurious trend, this result suggests that old immature herring are subject to a higher exploitation pressure than usually acknowledged.

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 life-history parameters and 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. Also temperature effects on growth can be taken into account. A version of this model has been parameterized for Northeast Arctic cod: analysis of 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.

Table 1. Fish populations where probabilistic maturation reaction norms have been estimated from time series data.

Species	Population or stock	Period with data	Trend towards earlier maturation?	Reference
Atlantic cod <i>Gadus morhua</i>	Northeast Arctic	1932–1998	Yes	Heino et al. 2002c
	Georges Bank	1970–1998	Yes	Barot et al. 2004b
	Gulf of Maine	1970–1998	Yes	
	Northern (2J3KL)	(1977–)1981–2002	Yes	Olsen et al. 2004
	Southern Grand Bank (3NO)	1971–2002	Yes	Olsen et al., in prep.
	St. Pierre Bank (3Ps)	1972–2002	Yes	
Plaice <i>Pleuronectes platessa</i>	North Sea	1957–2001	Yes	Grift et al. 2003
American plaice <i>Hippoglossoides platessoides</i>	Labrador–NE Newfoundland (2J3K)	1973–1999	Yes	Barot et al. 2004c
	Grand Bank (3LNO)	1969–2000	Yes	
	St. Pierre Bank (3Ps)	1972–1999	Yes	
Atlantic herring <i>Clupea harengus</i>	Norwegian spring-spawning	1935–2000	Yes, weak	Engelhard & Heino 2004
Grayling <i>Thymallus thymallus</i>	Lake Lesjaskogsvatnet, Norway	1903–2000 (ca. 15 years)	Yes	Haugen & Vøllestad, in prep.

## 5. Concluding remarks

Changes in age and size at maturation are widespread among commercially exploited fish stocks (Trippel 1995). Reaction norm analyses suggest that these trends are often seriously exacerbated by fisheries-induced evolutionary changes, unfolding on top of the direct demographic and phenotypically plastic effects of fishing. Any long-term analyses of population trends in fish stocks therefore need to be based on the realization that the maturation characteristics of fish stocks are far from being static. Instead, these characteristics dynamically vary with environmental conditions, due to phenotypic plasticity, and with exploitation regimes, due to evolutionary changes.

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