

# **Fisheries-induced evolution and sexual dimorphism in North Sea plaice**

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## **Goal**

To develop a multi-trait individual-based eco-genetic model for studying fisheries-induced evolution in North Sea plaice as documented by empirical data over the last century, with particular consideration of sex-specific mortality regimes and life-history responses.

## **Background and motivation**

### ***Fisheries-induced life history evolution***

Selective exploitation of fish stocks is increasingly recognized as driving the evolution of life history traits (Stokes et al., 1993). Higher mortality in general, and positively size-selective mortality in particular, cause an organism's current reproduction to become relatively more important than its future reproduction (Heino and Kaitala, 1999). This may result in slower growth rates, maturation at younger ages and smaller sizes, and a higher relative reproductive investment (Roff, 1983). Accordingly, size-selective harvesting has been shown to be associated with changes in growth and maturation (Sinclair et al., 2002; Grift et al., 2003; Conover et al., 2005; Olsen et al., 2005). However, measuring life history trait combinations of individual animals in the field is notoriously difficult, as one would ideally have to follow individuals throughout their life, and also since changes in life history traits are often confounded by phenotypic plasticity due to environmental variation.

Since life history changes due to size-selective fishing typically go along with a reduction of sustainable yield (Law and Grey, 1989; Heino and Godø, 2002), it is of interest to adopt management strategies to let fish stocks with evolved life history traits recover, or at least to prevent further life history changes. Individual-based eco-genetic models provide a powerful tool for understanding and analyzing the evolution of life-history traits, their correlation structure, and the effects of different harvesting strategies.

### ***North Sea plaice***

Plaice are sexually dimorphic: females grow faster, become mature at larger sizes and older ages, and allocate more energy to reproduction than males (Rijnsdorp and Ibelings, 1989). Growth rates are expected to be dependent on population density (Beverton, 1964), and changes in the productivity of the ecosystem might also play a role (Rijnsdorp and Van Beek, 1991). From the early 1900s to the mid-1980s female length and age at maturation had decreased by 10–16% and 30–35%, respectively, whereas male length and age at maturation had decreased by 35% and 50–60%, respectively (Rijnsdorp, 1989). Although changes in fecundity might partly reflect changes in the trade-off between egg size and egg number, the hypothesis of a fisheries-induced increase in reproductive investment in adult females (smaller than 50cm) seems empirically supported (Rijnsdorp, 1991).

North Sea plaice has been exploited substantially already since the late 19th century (Rijnsdorp and Millner, 1996). Landing statistics collected by ICES since 1906 show that annual plaice landings varied around 50,000t annually until the mid-1950s, after which landings peaked at 150,000t in the 1980s and since then decreased to the present 55,000t (ICES, 2006). Commercial landings have been extensively sampled since 1957. While mortality rates for males and females are similar during the growing season from April to December, they almost quadruple for males, but just about double for females, during the spawning season from January to March (Rijnsdorp, 1993). This is in accordance with the finding that males spend much more time on the heavily exploited spawning grounds than females (Rijnsdorp, 1989).

### ***Hypotheses on sexual dimorphism***

Female fish usually have a high advantage of increased body size, since egg viability and total fecundity typically increase with maternal size (Trippel and Neil, 2004). Selection on male size is also driven by female preference, by male-male competition for females, or by sperm competition for eggs (Parker, 1993; Ball and Parker, 1996). If male-male competition and sperm competition are very weak, small or even dwarf males are predicted to arise evolutionarily (Parker, 1992). Selection then also favors early maturation to increase the reproductive lifespan.

If males are small, it seems at first sight paradoxical that their surplus energy resulting from a smaller cost of reproduction as compared to females is not invested into somatic growth. This apparent paradox might be resolved by stipulating a lower growth efficiency in males (Henderson et al., 2003) or by assuming male investment into a behavioral trait related to reproduction. Since male North Sea plaice stay longer on the spawning ground than females (Rijnsdorp, 1989), we might assume that for North Sea plaice this behavioral trait is described by the duration of staying on the spawning grounds. This duration is most likely positively correlated with the number of reproductive events and with the amount of sperm produced. Since male plaice are clearly smaller than females, the general theory No empirical evidence suggests that male-male competition is rather weak. But sperm competition might be important, since more sperm production associated with a longer stay on the spawning grounds will cause more fertilizations.

However, any sexual size dimorphism (SSD) is also affected by the ratios between sex-specific growth rates and mortalities (Parker, 1992). Since mortality in male plaice is highest during the spawning period (Rijnsdorp, 1993), it seems likely that the considered behavioral trait is associated with higher mortality rates due to a higher exposure to fishing gear and predators. The selection imposed by sperm competition, favoring larger size, is therefore counterbalanced by the selection imposed by higher mortality, favoring smaller size. We assume that this trade-off acting on the male reproductive behavior mainly determines the observed SSD of plaice.

If positively size-selective mortality in a size-dimorphic population increases, one would expect larger evolutionary responses in the larger sex. Apparently, in the case of North Sea plaice, the opposite has happened: changes in the onset of maturation are dramatically larger in males than in females (Rijnsdorp, 1989). This might be explained by the fact that male plaice experience a steeper increase of mortality rates on the spawning grounds, and are thus more affected by fishing mortality.

By considering a male behavioral trait measuring the duration males spend on the spawning grounds, we will try to capture two trade-offs: longer stays on the spawning grounds imply a time cost (resulting in higher mortality), as well as an energy cost (resulting in diminished surplus energy, and thus potentially in reduced growth).

**Table 1:** Summary of observations related to SSD in the North Sea plaice fishery, of causes that may underlie these observations, and of approaches to how the latter could be accounted for in a model.

<b>Observation</b>	<b>Presumed causes</b>	<b>Modeling approach</b>
Males experience higher natural and fishing mortality	Males are more exposed to predators and fishing gear due to their spawning activity	Natural and fishing mortality in the model will differ between the sexes
Males stay longer on the spawning grounds	Selection for more time spent on the spawning grounds, since reproductive success is positively correlated with this duration	Male reproductive investment in the model will include investment into gonads and male reproductive behavior
Males are smaller at age	Stronger selection for early maturation, and thus indirectly for reduced growth, due to higher mortality and lower energetic costs of reproduction; direct selection for reduced growth because of higher mortality and larger investment into spawning activity	Model will incorporate selection for early maturation and for lower growth rate due to higher mortality associated with male reproductive behavior; energy lost on male reproductive behavior will slow down growth
Males mature earlier	Stronger selection for early maturation due to higher mortality and lower energetic costs of reproduction	Model will incorporate selection for early maturation, smaller gonads, and smaller body size based on assuming time and energy costs associated with male reproductive behavior
Males show a stronger response to size-selective harvesting	Steeper increase of male mortality rates on the spawning grounds due to their spawning activity	Model will incorporate separate mortalities for males and females on feeding and spawning grounds

In addition, also the trade-offs between gonadic investment and growth and between growth and survival will be considered. On this basis, we will attempt to test the following two hypotheses:

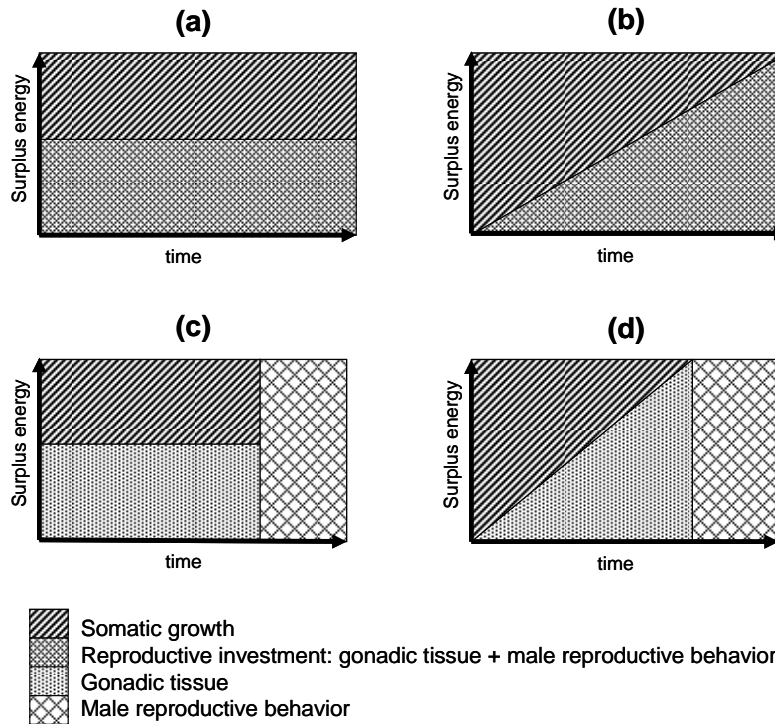
- (1) Selection on male reproductive behavior – involving two trade-offs, between fecundity on the one hand and mortality and growth on the other – can explain the observed SSD in North Sea plaice.
- (2) The higher exposure of males to fishing mortality on the spawning grounds can explain their larger life history response to exploitation.

This test will be based on reconstructing the observations in the fishery with the help of an eco-genetic model for North Sea plaice. Table 1 summarizes the most striking observations concerning the SSD in North Sea plaice and suggests how these could be reflected in the model.

## Research questions

### *Questions for devising an eco-genetic model for female plaice*

- How do we set up an eco-genetic model to recover the observed life history of female plaice?
- Which adaptive traits should be considered?
- Can we recover the observed changes in female life history and the pace of evolution induced by size-selective harvesting?



**Figure 1:** Possible patterns for the seasonal allocation of surplus energy to somatic growth and reproduction. Spawning occurs at the end of the shown time intervals. Surplus energy is assumed to be constant throughout the year. For females, only options (a) and (b) are considered, since reproductive investment in females solely consists of building gonadic tissue. For males, the reproductive investment in (a) and (b) has to be interpreted as the sum of energy used, in parallel, for gonadic tissue and male reproductive behavior. In (c) and (d), energy allocation to gonadic tissue and male reproductive behavior instead is sequential, and hence the behavioral reproductive investment can be disentangled from investment into gonadic tissue by allowing for a flexible date for the onset of this behavioral reproductive investment.

### *Questions for extending this model to capture the SSD*

- How do we have to define, separately for each sex, adaptive traits, life-history parameters, and trade-offs, in order to recover the sexual size dimorphism?
- Can the trade-offs involved in male reproductive behavior, as described above, explain the observed SSD?
- Can we recover the observed changes in male life history and the pace of evolution induced by sex-specific and size-selective harvesting?
- Can we recover, in particular, the observed stronger effect of size-selective harvesting on males?
- What is the relative evolutionary importance of the time costs and the energy costs associated with male reproductive behavior?
- Can selection on one sex affect evolution in the other sex?
- Are fisheries-induced evolutionary responses in this population amplified by the SSD?
- Which management measures could be adopted to mitigate fisheries-induced evolution in sexually size-dimorphic populations such as North Sea plaice?

## Methods and work plan

### *Eco-genetic model*

To study the effect of size-selective harvesting in a sex-structured population, we will devise an individual-based eco-genetic model (Dunlop et al., 2007) for North Sea plaice. This model will include phenotypic plasticity in age and size at maturation and will allow somatic growth to be density-dependent. As described above, we will also include the trade-offs involved in the evolution of male reproductive behavior and thereby go beyond previous models of mortality-induced evolution (Roff, 1983; Martinez-Garmendia, 1998).

To model somatic growth, we will use a simplification of the integrated energy allocation model by West et al. (2001), in which growth is defined in terms of the rate of change in somatic weight  $w$ ,  $dw/dt = aw^\alpha - cw^\gamma$ , where  $t$  is continuous time (or age),  $a$  scales the net energy intake, accounting for the costs of maintenance,  $c$  scales reproductive investment, and  $\alpha$  and  $\gamma$  are the corresponding allometric exponents. Parameters  $a$ ,  $c$ , and  $\alpha$ , will be taken from empirical studies (Fonds et al., 1992; Mollet et al., in prep.), while  $\gamma$  is assumed to be 1. Reproductive investment for males will be interpreted to comprise both the investment into gonadic tissue (as measured by GSI) and the investment into reproductive behavior. We will assume a parallel allocation of energy into somatic and reproductive investment. Different options for the underlying partitioning are illustrated in Figure 1. A constant condition factor  $\theta$  and shape parameter  $\lambda$  will be assumed to convert weight  $w$  to length  $l$ ,  $w = \theta l^\lambda$ .

The transition from the juvenile to the adult part of the life cycle will be determined by a maturation reaction norm, predicting the phenotypically plastic response of age and size at maturation to environmental variation in somatic growth rates (Stearns and Koella, 1986; Ernande et al., 2004). A recently developed probabilistic extension models the probability to mature as a function of age and size (Heino et al., 2002; Barot et al., 2004). For the sake of simplicity, we will assume linear reaction norms described by their intercept  $b$ , slope  $m$ , and width  $e$ .

A quantitative genetic approach will be used to implement inheritance and express heritability in the evolving traits  $a$ ,  $c$ ,  $b$ ,  $m$ , and  $e$ . Genetic variance will be represented by the distribution of trait values in the population (Van Noordwijk, 1989), whereas phenotypic variance resulting from environmental factors has to be assumed such that realistic values of heritability are obtained (Mousseau and Roff, 1987). The inheritance of quantitative traits in the offspring will be assumed to be equally determined by maternal and paternal trait values. In particular, the traits of each offspring will be drawn from a normal distribution with the mid-parental value as the mean. In sex-structured populations sex-specific traits will be considered.

Fecundity will be described by an allometric relation with respect to body size, while male reproductive success will depend, in addition, on assumptions made about the ecological implications of the duration males spend on the spawning grounds. Importantly, mating will not be assumed to be size-dependent, but random. The number of new individuals recruiting to the population at age 1 will be determined from a Beverton-Holt stock-recruitment function. Population dynamics will be based on annual time steps for growth, maturation, reproduction, and mortality.

### ***Work plan***

As a first step, we will try to recover the historical pattern of life history evolution in female plaice. The life history in the initial population will be matched to historical observations (Wallace, 1914).

As a second step, we will investigate simplified eco-genetic models for male plaice that (i) do not contain females explicitly and that (ii) do not describe male reproductive behavior through a separate adaptive trait (Figs. 1a and 1b). This implies assuming a constant fractional allocation of reproductive investment to male gonadic tissue and male reproductive behavior.

Time permitting, we might relax, as a third step, assumption (i) by analyzing sex-structured populations (as it might turn out that male and female life histories cannot be modeled independently from each other) and assumption (ii) by introducing a separate adaptive trait for male reproductive behavior (Figs. 1c and 1d).

Traits that might evolve in these models are thus the intrinsic growth rate ( $a$ ), reaction norm parameters ( $b$ ,  $m$ , and  $e$ ), reproductive investment ( $c$ ) and, if time permits, male reproductive behavior. Model predictions will be compared to empirical observations and to the result of previous studies, e.g., changes in  $a$  to a study by Rijnsdorp and Van Beek (1991), changes in  $b$  and  $m$  to a study by Grift et al. (2003), and changes in  $c$  to a study by Rijnsdorp et al. (2005). Empirical evidence for changes in male reproductive behavior might be obtained by analyzing changes in male mortality. In the longer term, also known changes in environmental conditions could be incorporated, like the absence of fishing during the world wars, the increasing fishing pressure in the early 1960s, or the high eco-system productivity in the 1960s.

### **Relevance and link to EEP's research plan**

This project aims to evaluate the ecological and evolutionary effects of size-selective fishing in a sexually size-dimorphic population and is therefore directly linked to EEP's focus on evolutionary fisheries management. If observations on North Sea plaice can be reproduced, this could provide further evidence of fisheries-induced evolution and offer insights into the evolutionary origins and implications of sexual size dimorphisms. Studying fisheries-induced evolution in sex-structured population models that account for the trade-offs associated with male reproductive behavior is a novel contribution to existing applications of eco-genetic models.

### **Expected output and publications**

This work will be included as a chapter in my PhD thesis and is intended for publication as a co-authored research article.

### **References**

- Ball, M.A. and Parker, G.A. (1996). Sperm competition games: external fertilization and "adaptive" infertility. *Journal of Theoretical Biology*, 180: 141-150.
- Barot, S., Heino, M., O'Brien, L. and Dieckmann, U. (2004). Estimating reaction norms for age and size at maturation when age at first reproduction is unknown. *Evolutionary Ecology Research*, 6: 659-678.
- Beverton, R.J.H. (1964). Differential catchability of male and female plaice in the North Sea and its effect on estimates of stock abundance. *Rapports et Procès verbaux des Réunions - Conseil permanent international pour l'Exploration de la Mer*, 155: 103-112.

- Conover, D.O., Arnott, S.A., Walsh, M.R. and Munch, S.B. (2005). Darwinian fishery science: lessons from the Atlantic silverside (*Menidia menidia*). Canadian Journal of Fisheries and Aquatic Sciences, 62: 730-737.
- Dunlop, E.S., Shuter, B.J. and Dieckmann, U. (2007). Demographic and evolutionary consequences of selective mortality: predictions from an eco-genetic model of the smallmouth bass. Transactions of the American Fisheries Society, 136: 749-765.
- Ernande, B., Dieckmann, U. and Heino, M. (2004). Adaptive changes in harvested populations: plasticity and evolution of age and size at maturation. Proceedings of the Royal Society of London, Series B, 271: 415-423.
- Fonds, M., Cronie, R., Vethaak, A.D. and Van der Puyl, P. (1992). Metabolism, food consumption and growth of plaice (*Pleuronectes platessa*) and flounder (*Platichthys flesus*) in relation to fish size and temperature. Netherlands Journal of Sea Research, 29: 127-143.
- Grift, R.E., Rijnsdorp, A.D., Barot, S., Heino, M. and Dieckmann, U. (2003). Fisheries-induced trends in reaction norms for maturation in North Sea plaice. Marine Ecology Progress Series, 257: 247-257.
- Heino, M., Dieckmann, U. and Godø, O.R. (2002). Measuring probabilistic reaction norms for age and size at maturation. Evolution, 56: 669-678.
- Heino, M. and Godø, O.R. (2002). Fisheries-induced selection pressures in the context of sustainable fisheries. Bulletin of Marine Science, 70: 639-656.
- Heino, M. and Kaitala, V. (1999). Evolution of resource allocation between growth and reproduction in animals with indeterminate growth. Journal Evolutionary Biology, 12: 423-429.
- Henderson, B.A., Collins, N., Morgan, G.E. and Vaillancourt, A. (2003). Sexual size dimorphism of walleye (*Stizostedion vitreum vitreum*). Canadian Journal of Fisheries and Aquatic Sciences, 60: 1345-1352.
- ICES (2006). Report of the working group on the assessment of demersal stocks in the North Sea and Skagerrak. ICES CM 2006/ACFM:09.
- Law, R. and Grey, D.R. (1989). Evolution of yields from populations with age-specific cropping. Evolutionary Ecology, 3: 343-359.
- Martinez-Garmendia, J. (1998). Simulation analysis of evolutionary response of fish populations to size-selective harvesting with the use of an individual-based model. Ecological Modelling, 111: 37-60.
- Mollet, F.M., Brunel, T., Ernande, B. and Rijnsdorp, A.D. Estimating onset of reproduction, reproductive investment and growth rate from individual growth trajectories, in preparation.
- Mousseau, T.A. and Roff, D.A. (1987) Natural selection and the heritability of fitness components. Heredity, 59: 181-197.
- Olsen, E.M., Lilly, G.R., Heino, M., Morgan, M.J., Brattey, J. and Dieckmann, U. (2005). Assessing changes in age and size at maturation in collapsing populations of Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences, 62: 811-823.
- Parker, G.A. (1992). The evolution of sexual size dimorphism in fish. Journal of Fish Biology, 41: 1-20.

- Parker, G.A. (1993). Sperm competition games - sperm size and sperm number under adult control. *Proceedings of the Royal Society of London, Series B*, 253: 245-254.
- Rijnsdorp, A.D. (1991). Changes in fecundity of female North-Sea plaice (*Pleuronectes platessa* L) between 3 periods since 1900. *ICES Journal of Marine Sciences*, 48: 253-280.
- Rijnsdorp, A.D (1993). Selection differentials in male and female North Sea plaice *Pleuronectes platessa* L. In: Stokes, T.K.A., McGlade, J. and Law, R. (eds.) *The exploitation of evolving resources*. Springer Verlag, pp. 19-36.
- Rijnsdorp, A.D. (1989). Maturation of male and female North-Sea plaice (*Pleuronectes-Platessa* L). *Journal Du Conseil*, 46: 35-51.
- Rijnsdorp, A.D., Grift, R.E. and Kraak, S.B.M. (2005). Fisheries-induced adaptive change in reproductive investment in North Sea plaice (*Pleuronectes platessa*)? *Canadian Journal of Fisheries and Aquatic Sciences*, 62: 833-843.
- Rijnsdorp, A.D. and Ibelings, B. (1989). Sexual dimorphism in the energetics of reproduction and growth of North Sea plaice, *Pleuronectes-Platessa* L. *Journal of Fish Biology*, 35: 401-415.
- Rijnsdorp, A.D. and Millner, R.S. (1996). Trends in population dynamics and exploitation of North Sea plaice (*Pleuronectes platessa* L) since the late 1800s. *ICES Journal of Marine Sciences*, 53: 1170-1184.
- Rijnsdorp, A.D. and Van Beek, F.A. (1991). Changes in growth of plaice *Pleuronectes platessa* L and sole *Solea solea* (L) in the North Sea. *Netherlands Journal of Sea Research*, 27: 441-457.
- Roff, D.A. (1983). An allocation model of growth and reproduction in fish. *Canadian Journal of Fisheries and Aquatic Sciences*, 40: 1395-1404.
- Sinclair, A.F., Swain, D.P. and Hanson, J.M. (2002). Measuring changes in the direction and magnitude of size-selective mortality in a commercial fish population. *Canadian Journal of Fisheries and Aquatic Sciences*, 59: 361-371.
- Stearns, S.C. and 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.
- Stokes, T.K., McGlade, J.M. and Law, R. (1993). *The exploitation of evolving resources*. Springer-Verlag.
- Trippel, E.A. and Neil, S.R.E. (2004). Maternal and seasonal differences in egg sizes and spawning activity of northwest Atlantic haddock (*Melanogrammus aeglefinus*) in relation to body size and condition. *Canadian Journal of Fisheries and Aquatic Sciences*, 61: 2097-2110.
- Van Noordwijk, A.J. (1989). Reaction norms in genetic ecology - studies of the great tit exemplify the combination of ecophysiology and quantitative genetics. *Bio-science*, 39: 453-458.
- Wallace, W. (1914). Report on age and growth and sexual maturity of the plaice in certain parts of the North Sea. *Fisheries Investigation Series*, 2: 79.
- West, G.B., Brown, J.H., Enquist, B.J. (2001). A general model for ontogenetic growth. *Nature*, 413: 628-631